# Journal of the Entomological Society of British Columbia

Volume 99
Issued December 2002

ISSN #0071-0733

ESBC

***COVER*:** An apterous vivipara of *Myzus persicae* (Sulzer) feeding on the leaf of Chinese pe-tsai, *Brassica pekinensis* (Loureiro) Ruprecht, 70× magnification.

**Scanning electron microscopy**. Live green peach aphid feeding on Chinese pe-tsai leaf was transferred to an aluminum tape-rimmed SEM stub. The loaded stub and its holder were placed in the specimen chamber, viewed and pictured with a Hitachi S-500 SEM at an accelerating voltage of 15 kv under vacuum.

**Remark.** Cho-kai Chan took this picture in 1979, and won the competition of insect photo contest during an ESBC annual general meeting in the early 1980's. The judge was SFU's renowned photographer, Mr. Ron Long. This picture was then used as a logo on the pamphlet for the Agriculture Canada Vancouver Research Station. Cover photo and text by Cho-kai Chan.

The Journal of the Entomological Society of British Columbia is published annually in December by the Society

Designed and typeset by Ward Strong and David Holden.
Printed by Reprographics, Simon Fraser University, Burnaby, BC, Canada.

Printed on Recycled Paper.

# Journal of the Entomological Society of British Columbia

Volume 99 Issued December 2002 ISSN #0071-0733

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# Homoptera (Insecta) in Pacific Northwest grasslands. Part 1 – New and revised taxa of leafhoppers and planthoppers (Cicadellidae and Delphacidae).

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## ABSTRACT

Nine new combinations are created when *Acanthodelphax* LeQuesne (Delphacidae) is synonymized with *Kosswigianella* Wagner and the genus *Aschedelphax* Wilson is reduced to subgenus in *Elachodelphax* Vilbaste: *Delphacodes analis* Crawford and three Palaearctic species in *Acanthodelphax* are transferred to *Kosswigianella*; *Aschedelphax hochae* Wilson, *Delphacodes coloradensis* Beamer, *D. indistinctus* Crawford, *D. bifidus* Beamer, and *D. pedaforma* Beamer are transferred to *Elachodelphax*. Seven other new combinations include *Delphacodes atridorsum* Beamer, transferred to *Caenodelphax* Fennah; *Delphacodes kilmani* (Van Duzee), transferred to *Paraliburnia* Jensen-Haarup; *Delphacodes venusta* Beamer, transferred to *Nothodelphax* Fennah; *Eurysa magnifrons* (Crawford), *E. montana* Beamer and *E. obesa* Beamer, transferred to *Eurybregma* Scott; plus the leafhopper *Sorhoanus helvinus* (Van Duzee) transferred to *Lebradea* Remane. Twenty new species and 3 new subspecies are described from the Pacific Northwest, including the leafhoppers *Athysanella castor*, *A. hyperoche, A. lemhi, A. occidentalis megacauda*, *A. repulsa*, *Diplocolenus configuratus bicolor*, *Mocuellus caprillus anfractus*, *M. quinquespinus, Psammotettix diademata*, *P. nesiotus*, *Sorhoanus involutus*, *S. virilis*, *S. xiphosura*, *Stenometopiellus vader* and *Unoka dramatica*, plus the planthoppers *Achorotile apicata*, *Elachodelphax unita* and *E. mazama* (both compared to *E. borealis* sp. nov. from east of the Rocky Mountains), *Eurybregma eurytion*, *Kosswigianella irrutilo*, *K. wasatchi*, *Paraliburnia furcata* and *P. lecartus*. Two new names are created: *Athysanella (Gladionura) hicksi* for *A. expulsa* Blocker and Hicks (preoccupied), and *Psammotettix greenei* for *P. emarginata* Greene (preoccupied). The presence of intermediate morphs suggestive of hybrids reduce *Athysanella ladella* Johnson and *A. wilburi* Ball & Beamer to subspecific status in *A. occidentalis* Baker, *Diplocolenus nigrior* Ross & Hamilton to subspecies status in *D. configuratus* (Uhler) and *Mocuellus strictus* Ross & Hamilton to subspecies status in *M. caprillus* Ross & Hamilton. Variation within series over a wide area reduces *Athysanella vativala* Blocker to synonymy with *A. terebrans* Gillette & Baker, and *A. mansa* is synonymized with *A. occidentalis wilburi* as a hybrid morph.

## INTRODUCTION

Grasslands form a minor part of the rugged landscape of the Pacific Northwest (PNW). They are restricted to favourable elevations sandwiched between huge areas of coniferous forest and sagebrush semidesert. The elevation of these grasslands varies with both latitude and local topography. In the southern Okanagan Valley of British Columbia (latitude 49°) the following communities are generally found on west-facing slopes at the following elevations: sagebrush steppe to 350 m; steppe-grassland ecotone, to 700 m; Palouse grassland to 800 m; grassland-forest ecotone to 1000 m. At Bannock Pass on the Idaho-Montana border (latitude 45°) sagebrush steppe reaches 2000 m and forests begin again just above the pass (2200 m), compressing grassland and its ecotones into a few hundred metres. South-facing slopes can raise the elevation of the grassland community as much as 200 m. Conversely, grasslands are often absent on steep north-facing slopes.

Much of these grasslands have been converted to agriculture, or confined to small patches in intermontane valleys, dissected by deep canyons, or separated by mountain ranges. Pacific Northwest grasslands extend over six states and two provinces. Their main mass runs from isolated valleys of central British Columbia (BC) south to the Palouse hills of Washington (WA) and the Snake River plains of Idaho (ID), and down the foothills of the Cascade Mountains to Oregon (OR). Patches of this grassland may be found on mountains of Colorado (CO), Utah (UT) and Wyoming (WY). On the eastern slopes of the Rocky Mountains a similar grassland extends from southwestern Alberta (AB) to southern Montana (MT).

PNW grasslands are home to many grassland-endemic phytophagous insects. The most numerous species of these endemics belong to the leafhopper family Cicadellidae (Figs. 1-2). Leafhoppers are diverse, with over 2000 species in North America (Oman 1949). A large proportion of these are grassland insects (Ross 1970) which include more than 150 species monophagous on grasses (Hamilton and Whitcomb 1993) and many others oligophagous on arid-adapted forbs, principally composites such as sagebrush, *Artemisia* spp., balsamroot, *Balsamorhiza* spp. and rabbitbrush, *Chrysothamnus* spp. (Hamilton 1998*a*, Hamilton and Zack 1999).

The leafhopper fauna we find today in the PNW has a high percentage of endemic species. A smaller number of leafhopper species are widely dispersed across many habitat types. These have little to tell us about historical biogeography. For example, species of *Helochara* Fitch (Hamilton 1986, maps 17-18) which are not restricted to prairie plants range far outside native grasslands.

The purpose of this paper is to present new and revised taxa of PNW endemic leafhoppers and planthoppers (Fulgoroidea) of the family Delphacidae (Fig. 3). The second part analyses their biogeography, together with that of planthoppers of the family Caliscelidae (Fig. 4), for evidence of endemism and postglacial spread. These planthoppers, although fewer in number and less studied than leafhoppers, show similar dispersal patterns and thus are included in this analysis.

## METHODS

Numerous leafhopper and planthopper species inhabit prairies and semidesert grasslands adjacent to the PNW, but have no populations in the PNW. They are therefore excluded from this study. These include the leafhopper genera *Dicyphonia* Ball, *Driotura* Osborn & Ball, *Extrusanus* Oman, and various genera of the Sonoran subregion. Nevertheless, hundreds of grassland-endemic leafhopper and planthopper species do inhabit PNW grasslands, permitting detailed analysis of their known distributions.

The few PNW species of the leafhopper genera *Acinopterus* Van Duzee, *Chlorotettix* Van Duzee, *Commellus* Osborn & Ball, *Endria* Oman, *Frigartus* Oman, *Hardya* Edwards, *Idiodonus* Ball, *Lonatura* Osborn & Ball, *Lystridea* Baker, *Mesamia* Ball, *Paluda* DeLong, *Pinumius* Ribaut, *Stragania* Stål, *Twiningia* Ball and *Xerophloea* Germar are distinctive (Oman 1949; Beirne 1956) and present no taxonomic problems to the biogeographer. Revisionary work has been done for the more complex leafhopper genera *Amblysellus* Sleesman (Kramer 1971), *Athysanella* Baker (Blocker and Johnson 1988, 1990*a, b, c*; Blocker and Hicks 1992), *Attenuipyga* Oman (Hamilton 2000), *Auridius* Oman (Hamilton 1999), *Balclutha* Kirkaldy (Hamilton 1983), *Carsonus* Oman (1938), *Ceratagallia* Kirkaldy (Hamilton 1998*a*), *Colladonus* Ball (Nielson 1957), *Cuerna* Melichar (Hamilton 1970), *Diplocolenus* Ribaut (Ross and Hamilton 1970*a*), *Draeculacephala* Ball (Hamilton 1985), *Elymana* DeLong (Chiykowski and Hamilton 1985), *Errhomus* Oman (Hamilton and Zack 1999), *Euscelis* Brullé and *Evacanthus* LePeletier & Serville (Hamilton 1983), *Flexamia*

DeLong (Whitcomb and Hicks 1988), *Gyponana* Ball (Hamilton 1982), *Hebecephalus* DeLong (Hamilton 1998*b*), *Hecalus* Stål (Hamilton 2000), *Laevicephalus* DeLong (Ross and Hamilton 1972*a*), *Latalus* DeLong & Sleesman (Ross and Hamilton 1972*b*), *Limotettix* Sahlberg (Hamilton 1994), *Mocuellus* Ribaut (Ross and Hamilton 1970*b*), *Norvellina* Ball (Lindsay 1940), *Orocastus* Oman (Beirne 1956; Ross and Hamilton 1972*b*), *Paraphlepsius* Baker (Hamilton 1975), *Prairiana* Ball (DeLong 1942), *Psammotettix* Haupt (Greene 1971), *Rosenus* Oman (Ross and Hamilton 1975), *Scaphytopius* Ball (Hepner 1947), *Texananus* Ball (Crowder 1952); in Caliscelidae, *Bruchomorpha* Newman (Doering 1940); and among Delphacidae, *Eurysa* Fieber (Beamer 1952), *Laccocera* Van Duzee (Scudder 1963), and *Pissonotus* Van Duzee (Bartlett and Deitz 2000).

The first part of this study comments on the taxonomy of the leafhopper genera *Athysanella* (with four new species and one new subspecies), *Mocuellus* and *Sorhoanus* Ribaut (each with three new species), *Psammotettix* (two new species and one new name), *Stenometopiellus* Haupt and *Unoka* Lawson (each with one new species), and *Diplocolenus* (one new subspecies). One Delphacid is newly assigned to *Nothodelphax* Fennah, and eight others to four genera that are recorded from the Nearctic for the first time: *Elachodelphax* Vilbaste, *Eurybregma* Scott, *Kosswigianella* Wagner and *Paraliburnia* Jensen-Haarup. Eight new Delphacid species are described in *Elachodelphax* subgenus *Aschedelphax* Wilson, stat.nov. (three new species), *Kosswigianella* and *Paraliburnia* (each with two new species), and *Eurybregma* (with one new species).

## CICADELLIDAE

Cicadellid species are identified mainly by male genital structures (Figs. 5-37), although proportions of the head and colour patterns are sometimes useful. Many grassland leafhoppers feed on only one species (monophagous) or one genus of plant (oligophagous). This often helps resolve species complexes where morphologically similar insects have different biological requirements (see below). Leafhopper genera mentioned here are identifiable using keys presented by Oman (1949). The following leafhopper taxa represent two redefined genera, two new synonymies, two new names, 12 new species and three new subspecies.

### ***Athysanella* (*Athysanella*) *terebrans* (Gillette & Baker)**
(Figs. 5 A-E)

*Eutettix terebrans* Gillette & Baker, 1895: 102.
*Nephotettix terebrans*: Van Duzee 1917: 653.
*Athysanella terebrans*: Osborn 1930: 703 (misidentification of *A. fredonia* Ball & Beamer).
*Athysanella incongrua*: Osborn 1930: 703 (nec Baker, 1898).
*Athysanella vativala* Blocker [*in* Blocker and Johnson], 1988: 38 (**new synonymy**).

**Diagnosis.** This species has been much confused with other taxa. Because the holotype of *terebrans* is a female without associated male, its identity can be deduced only from colour, female genitalia and locality (North Park, Colorado). Lengthy series from northern prairie localities show that only a few species agree in all three particulars with the type of *terebrans*. *Athysanella incongrua* Baker (TX-CO) is eliminated because it is monophagous on little bluestem, *Schizachyrium scoparium* (Michx.) Nash, a grass that does not occur in Colorado. More southerly species, such as *A. laeta* Ball & Beamer (AZ-NM), are highly unlikely to occur at the type-locality in northern CO. This leaves only three possibilities (with south-to-north range in brackets):

(1) *Athysanella fredonia* Ball & Beamer (AZ-WY), monophagous on galleta, *Hilaria jamesii* (Torr.) Benth.

(2) *A. kadokana* Knull (CO-AB), monophagous on alkali grass, *Distichlis stricta* (Torr.) Rydb.;

(3) *A. vativala* Blocker (UT-AB), monophagous on sand grass, *Calamovilfa longifolia* (Hook.) Scribn.

Series of these three species taken on their hosts were examined to ensure that no mixing of populations had occurred. Only specimens of *A. vativala* match the figure of the female pregenital sternite in the type of *terebrans*, with long, conical lobes separated by a small median lobe. The lobes of *A. kadokana* and *A. fredonia* are low and rounded, and in the latter the median lobe is wide. Therefore the type of *terebrans* from Colorado is clearly conspecific with *A. vativala*.

The male genitalia of *A. terebrans* are similar to those of *A. incongrua* and *A. laeta*, but the latter characteristically have an apically enlarged aedeagus. The male characters cited by Blocker to differentiate “terebrans” from “vativala” are variable within lengthy series, for example in series collected on sand grass from 40 km S Orion, Alberta, from Colorado Springs, Colorado, and from Fertile, Minnesota (Figs. 5A-E) which represent the extremes of its distribution on the prairies. These forms therefore represent a single species.

### ***Athysanella (Amphipyga) occidentalis megacauda* ssp. nov.**

(Figs. 8 A-B)

**Etymology:** *mega*, large; *cauda*, tail, in reference to the aedeagal size.

**Adults**. Characters as in typical *A. occidentalis* Baker (Blocker and Johnson 1990*a*: 126, figs. 102-104), but aedeagus 1.4 × as long as in typical subspecies, and more evenly curved, with finer lateral serrations (Fig. 8A-B).

**Types**. Holotype male, **CANADA.** *BC*- Osoyoos IR 1, 119°29'W 49°04'N, 3 Oct. 1994-11 Apr. 1995 (G.G.E. Scudder) pitfall trap. Paratypes: 20 males, 1 female, 11 nymphs, same data as holotype; 3 males, 1 female, same data, 119°32'W 49°09'N, 31 May-5 July 1994; 7 males, 8 females, same data, 119°31'W 49°13'N, 2 June-7 July 1994; 1 male, 3 females, same data, 119°32'W 49°13'N, 7 July-4 Aug. 1994. All types No. 22831 in CNCI.

**Additional material:** 54 males, 55 females, 6 nymphs from **CANADA-** BC: Chopaka, Douglas Lake, Hedley, Kamloops, Lac du Boris, Oliver, Osoyoos, Penticton; **USA-** WA: Azwell, 9 km SW Havillah, 9 km NE Tonasket, 5 km NE Vantage.

**Diagnosis**. Populations of *A. occidentalis megacauda* from central WA to Kamloops, BC show little if any variation in aedeagal size. However, populations from the north side of the upper Snake River valley in ID and the Bitterroot valley in adjacent MT show evidence of introgression, having an aedeagus of intermediate length (0.40 mm) between the typical subspecies (aedeagal length 0.35 mm, Fig. 7) and the western *megacauda* (0.50 mm, Fig. 8).

Additional samples of *A. occidentalis* from ID and CO indicate there are two more subspecies, discussed below.

### ***Athysanella (Amphipyga) occidentalis ladella* Johnson, stat.nov.**

(Figs. 6 A-B)

*Athysanella ladella* Johnson [*in* Johnson and Blocker], 1979: 383.

**Diagnosis**. A population on the south side of the upper Snake River valley near the UT border is intermediate between *A. occidentalis megacauda* and *A. ladella*, a taxon described from southern NM. This population has a broader aedeagal shaft in caudal aspect (Fig. 6A-B) than that figured by Blocker and Johnson (1990, figs. 58-59) from the type series of *ladella*. This taxon therefore becomes a subspecies of *A. occidentalis* Baker (1898).

***Athysanella (Amphipyga) occidentalis wilburi* Ball & Beamer, stat.nov.**
*Athysanella wilburi* Ball & Beamer, 1940: 38.
*Athysanella mansa* Johnson [*in* Johnson and Blocker], 1979: 381, **syn.nov.**
**Diagnosis**. *A. wilburi* (described from Kansas) appears to hybridize occasionally with *occidentalis* where their ranges meet in CO. The intermediate form *mansa* Johnson & Blocker probably represents local hybrids, as all three taxa are known to occur together (e.g., at Ellicott, CO).

***Athysanella (Gladionura) hicksi* nom.nov.**
*A. (Gladionura) expulsa* Blocker and Hicks, 1992: 41, preoccupied; nec *A. (Amphipyga) expulsa* Blocker [*in* Blocker and Johnson], 1990: 112.
**Etymology:** patronym in honour of A.L. Hicks, who first found this species.

**Remarks.** This Californian species should not be confused with true *A. expulsa* from OR, discussed under *A. (Pedumella) repulsa* sp.nov.

***Athysanella (Gladionura) hyperoche* sp.nov.**
(Figs. 9 A-B)
**Etymology:** *hyperoche* (noun in apposition), summit; process.

**Adults**. Grey-green (body faded to tan) without definite dark markings, except median lobe of female pregenital sternite which is bordered with black. Ocellus very close to eye; crown obtusely pointed, 0.9 × as long as wide in male, 1.0-1.05 × in female, 0.75 × as long as pronotum in male, 0.67 × in female; hind tibial spur half as long as basitarsomere; female pregenital sternite as in *A. directa* Ball & Beamer (Blocker and Johnson 1990*b*, fig. 58), but central conical lobe longer, distinctly produced beyond low lateral angles; male subgenital plates large, longer than pygofers, divergent, apices sharp, directed outwards; pygofers apically rounded, with spine on upper margin at tip, directed caudodorsad, then hooked laterad (Fig. 9A), its length one-third that of pygofer; styles as in *A. concava* Ball & Beamer (Blocker and Johnson 1990*b*, fig. 66), but parallel-margined on apical half almost to narrowed, blunt tip (Fig. 9B); aedeagus smooth and parallel-margined, as in *concava* (idem, fig. 65). Length: male 2.9-3.2 mm, female 4.1-4.3 mm. Width of head: male 0.95-1.0 mm, female 1.05 mm; of crown between eyes: 0.50-0.55 mm, of pronotum: male 0.9-0.95 mm, female 0.95-1.0 mm.

**Types**. Holotype male, **USA.** *WY*- Laramie Mts. summit [on] I-80 [16 km SE Laramie, 2500m], 24 Aug. 1969 (Ross, Ross & Miller) GL 1161 ["heavily pastured range with a variety of close cropped grasses"]. Paratypes: 2 males, 2 females, same data as holotype. All types No. 22832 in CNCI.

**Diagnosis**. This species shares the rounded pygofer lobe and erect pygofer process of *A. falla* Blocker (Blocker and Johnson 1990*b*, figs. 72-73), but is distinguished by the much longer pygofer process (Fig. 9A) and style (Fig. 9B). From *A. concava* it is distinguished by the shorter, rounded pygofer with long, hooked dorsal process (in *A. concava* the pygofer is long, tapered to a short hook, as in Blocker and Johnson 1990*b*, fig. 68).

**Biology.** The types were taken along with two females of *A. robusta* Baker and one of *A. obesa* Ball & Beamer. These latter species are both specialists on June grass, *Koeleria macrantha* (Ledeb.) Schultes (=*K. cristata* auct.), a grass that is common in heavily grazed, arid sites. Therefore the host of this new species also may be the same grass.

***Athysanella (Pedumella) castor* sp.nov.**
(Figs. 11B-D, F)
**Etymology:** *castor* (noun in apposition), beaver; named for the Beaverhead Mountains that divide its range.

**Adults**. Grey-green with abdomen spotted and streaked with black, as in *A. obesa* (Beirne 1956, fig. 436); pleura and sternites often irregularly darkened; median lobe of female pregenital sternite contrastingly black. Ocellus very close to eye; crown parabolically produced, 0.9 × as long as wide, 1.5 × as long as pronotum; hind tibial spur absent; female pregenital sternite short, transverse or weakly emarginate laterally, median lobe prominent to large and rounded; male subgenital plates shorter than pygofers, divergent, apices sharp, directed caudad with small tooth on inner margin just before tip; pygofers tapered to small apical lobe with angle on lower margin at tip (as in Fig. 10A); ventral connective scarcely narrowed on apical half; styles in ventral aspect as in *A. attenuata* Baker (Blocker and Johnson 1990*a*, fig. 25), but with bladelike tip strongly produced as a flange on inner margin in widest aspect (Fig. 11F) and beyond this, tip tapered, curved ventrad; aedeagus curved cephalad, strongly widened apically, spatulate, bearing paired serrate ridges on anterior and caudal margins (Figs. 11B, D), in caudal aspect 4 × as long as wide. Length: male 3.1-3.6 mm, female 3.8-4.8 mm. Width of head: male 1.1-1.2 mm, female 1.2-1.25 mm; of crown between eyes: male 0.50-0.55 mm, female 0.55-0.60; of pronotum: male 0.9.5-1.05 mm, female 1.1-1.15 mm.

**Types**. Holotype male, **USA.** *MT*- Badger Pass N of Bannock, 31 May 1992 (K.G.A. Hamilton) [on *Festuca* mixed with *Agropyron*]. Paratypes: 6 males, 16 females, same data; 4 males,.8 females, *ID*- 8 km NE Carmen, 4 June 1992 (K.G.A. Hamilton); 1 female, *ID*- 11 km E Tendoy, 29 May 1995 (K.G.A. Hamilton). All types No. 22833 in CNCI.

**Diagnosis.** The spatulate aedeagus is distinctive, even when reduced in size by parasitism (Fig.11C).

**Remarks.** *A. castor* belongs to a group of species along with *A. attenuata*, *A. expulsa* Blocker and two new species (described below). All five of these species differ from other *Athysanella* in having a terminal gonopore and at least two pairs of serrated ridges on the aedeagus (Figs. 10-14). These are tentatively placed in the subgenus *Pedumella* (which presently has only two unrelated species) on the basis of their short pygofer process, tapered subgenital plates with two apical angles making them appear truncate at tips, and massive apical half of the ventral connective.

***Athysanella (Pedumella) lemhi* sp.nov.**
(Figs. 10 A-B, D-F)
**Etymology:** *Lemhi* (noun in apposition): this species is known only from just below Lemhi Pass.

**Adults**. Colour and form as in *A. castor*, but male sometimes (type) with crescent-shaped coronal marks; crown more obtuse, 0.8 × as long as wide, 1.25 × as long as pronotum; female pregenital sternite variable, from narrowly and weakly produced medially, to broadly and triangularly produced; male subgenital plates shorter than pygofers, divergent, apices sharp, directed caudad with small tooth on inner margin just before tip; pygofers tapered to small apical lobe with angle on lower margin at tip (Fig. 10A); styles broadly spatulate in widest aspect (Fig. 10F); aedeagus curved cephalad, slightly widened apically, bearing paired serrate ridges on anterior margin and also laterally (Figs. 10B, D), in caudal aspect 3 × as long as wide. Length: male 3.5 mm, female 4.0-4.9 mm. Width of head: male 1.1 mm, female 1.25 mm; of crown between eyes: male 0.5 mm, female 0.55-0.6 mm; of pronotum: male 1.05 mm, of female 1.2 mm.

**Types**. Holotype male, **USA.** *ID*- 14 km E Tendoy [16 km by road], 29 May 1995 (K.G.A. Hamilton). Paratypes: 1 female, same data as holotype; 1 male, 8 females, 15 km E Tendoy [17 km by road], 5 June 1992 (K.G.A. Hamilton). All types No. 22834 in CNCI.

**Diagnosis**. This species has genitalia similar to those of *A. castor*, but the aedeagus is longer and straighter, with the serrate ridge placed laterally rather than along the caudal margin, and the enlarged style apex is spatulate rather than tapered beyond the flange.

***Athysanella (Pedumella) repulsa* sp.nov.**
(Figs. 14 B, D-G)
**Etymology:** *repulsa*, repelled; named for its allopatric distribution with respect to *A. expulsa*.

**Adults**. Female unknown. Male grey-green mottled with brown, including two crescentric marks on crown. Ocellus set further than 2 diameters from eye; crown bluntly angled, as long as wide, 1.3 × as long as pronotum; hind tibial spur absent; male subgenital plates short and lyriform, as in *A. expulsa*; pygofers tapered to small, but elongate apical lobe with dark tooth on lower margin at tip; styles tapered to sharp point in ventral aspect (Fig. 14G), with strongly produced flange on upper surface which makes style apex spatulate in widest aspect (Fig. 14F); aedeagus strongly curved cephalad, slender, slightly widening towards apex in lateral aspect, tip obliquely truncate, bearing paired serrate ridges on anterior and caudal margins (Fig. 14B), gonopore lying in shallow dorsal depression (Fig. 14D) at narrowed tip (Fig. 14E). Length to tip of wings: male 2.0 mm (estimated overall length 3.5 mm). Width of head 1.2 mm, of crown between eyes 0.50 mm, of pronotum 1.1 mm.

**Types**. Holotype male, **USA.** *MT*- 15 km W Philipsburg [1 mi E junction of Hwy. 348 and Upper Willow Creek Road], 1 June 1992 (K.G.A. Hamilton); No. 22835 in CNCI.

**Diagnosis**. This species has a pygofer lobe intermediate in size between those of *A. lemhi* (Fig. 10A) and *A. expulsa* (Blocker and Johnson 1990a, fig. 27). The aedeagal shaft is much narrower in both lateral and caudal aspect than in *expulsa* (Fig. 12B), more closely resembling that of *A. attenuata* (Fig. 13B), but without lateral flanges. It shares with *A. expulsa* a style tip bearing a large flange on the upper surface and aedeagal shaft strongly curved, bearing serrate margins.

**Remarks.** *Athysanella repulsa* and *A. expulsa* are probably sister species. Each is known from a very limited geographical area. Their ranges are separated by the width of both the Columbia basin of OR and the Snake River plain of ID. In this respect they resemble the sister species *Auridius vitellinus* Hamilton and *A. cosmeticus* Hamilton which occur in the same widely separated localities.

***Diplocolenus configuratus bicolor* ssp.nov.**
(Fig. 15)
**Etymology:** *bicolor*, two toned; named for the unusual wing pattern (divided down the midlength) that occurs in half the population.

**Adults.** Two colour morphs in nearly equal proportions. *Pale morph:* uniformly tan, more or less mottled with brown as in typical *D. configuratus* (Uhler) (Beirne 1956, fig. 469); *bicolored morph:* head brown with pale coronal margins, body and basal half of tegmina blackish brown with narrow pale lines, apical half of tegmina contrastingly pale with brown mottling along veins. Male subgenital plates variable in length and shape of apices, as long as wide, tapered with tips truncate, or (especially in pale individuals) shorter and apically divergent as in typical subspecies (Ross and Hamilton 1970*a*, fig. 3C); pygofers shorter than subgenital plates, distinctly shorter than high, abruptly tapered to small apical spine at tip, ventral margin sinuate (Fig. 15); styles evenly tapered, as in typical subspecies (Ross and Hamilton 1970*a*, fig. 3B); aedeagus strongly curved in lateral aspect as in *D. nigrior* Ross and Hamilton (1972*b*, fig. 3), in caudal aspect widening towards apex, with divergent prongs at tip as in typical subspecies (Ross and Hamilton 1970*a*, fig. 3D). Length: male 3.3-3.8 mm, female 2.5-4.2 mm.

**Types**. Holotype male, bicolored morph, **USA.** *WY*- Wilson [W edge of town adjacent to Teton Pass grade] 14 June 1992 (K.G.A. Hamilton) [mainly on *Festuca*]. Paratypes: 19 nymphs, 30 bicolored and 33 pale males, 21 bicolored and 22 pale females, same data, No. 22836 in CNCI.

**Diagnosis**. The short pygofer with sinuate lower margin is distinctive, as is the bicolored morph. The genitalia most resemble those of *D. nigrior*, which is reduced to subspecific status (see below).

### ***Diplocolenus configuratus nigrior*** **Ross & Hamilton, stat.nov.**

*Diplocolenus nigrior* Ross & Hamilton, 1972*b*:442.

**Diagnosis**. The variability of the male subgenital plates suggests that the types are descendants of a hybrid swarm (*configuratus* × *bicolor*). If so, all three subspecies of *D. configuratus* appear to hybridize where their ranges abut. Strongly truncate subgenital plates (Fig. 16) indicate intermediates of *bicolor* × *nigrior* at 20 km E of Alpine, WY, and of *configuratus* × *nigrior* at Lemhi Pass and Spencer, ID. The aedeagus of all these intermediates resembles that of subspecies *bicolor*.

### **Genus *Lebradea* Remane, redefined**

*Lebradea* Remane, 1959: 386.Type-species by original designation, *L. calamagrostidis* Remane, 1959.

**Diagnosis.** By redefinition of *Sorhoanus* (see below), species of *Lebradea* are excluded from *Sorhoanus* (sensu lato of Oman 1949; Beirne 1956; Hamilton and Langor 1987). They are more slender, and have a distinctive female pregenital sternite with a long, median process (Beirne 1956, figs. 459, 761). Males are also differentiated in having pygofer setae confined to the caudal margin (Ossiannilsson 1983, fig. 2852) and in having the connective tip turned dorsad just before its articulation with the aedeagus, with the sides unconnected across the apex.

**Included species.** This small genus consists of the Holarctic *L. flavovirens* (Gillette & Baker), the Californian *L. helvina* (Van Duzee: *Thamnotettix*), **comb.nov.** from *Sorhoanus*, and three Old World species (Nast 1972).

### ***Mocuellus caprillus anfractus*** **spp. nov.**

(Figs. 17 A-B, 20)

**Etymology:** *anfractus*, crooked or twisted, in reference to the curved aedeagal shaft compared to that of *M. strictus* Ross & Hamilton, which is straight.

**Adults**. Tawny with indefinite pale brown markings; crown longer than midline of pronotum, as in typical *M. caprillus* Ross & Hamilton (Beirne 1956, fig. 448 "M. collinus"); genitalia as in typical *M. caprillus* (Ross & Hamilton 1970*b*, fig. 3B), but aedeagus in lateral aspect more sinuate throughout length (Fig. 17A), ventral teeth of similar size (Fig. 17B) and style tip with long, conical apical process (Fig. 20). Length to tip of pygofer (omitting setae): male 2.9-3.6 mm, female 3.3-4.2 mm.

**Types**. Holotype male, **USA.** *UT*- 7 km E Laketown, 13 June 1992 (K.G.A. Hamilton). Paratypes: 2 nymphs, 12 males, 9 females, same data as holotype; 1 male, *UT*- 23 km W Woodruff, 13 June 1992 (K.G.A. Hamilton); 3 males, 2 females, *ID*- 23 km SW Darlington, 7 June 1992 (K.G.A. Hamilton); 2 nymphs, 7 males, 1 female, *ID*- 12 km S Hamer, 19 June 1984 (K.G.A. Hamilton); 4 males, 2 females, *WY*- N of Jackson Hole, 15 Aug. 1971 (H.H. Ross) GL 1265 [on *Poa* and *Agropyron*]. All types No. 22837 in CNCI.

**Additional material:** 5 females (without associated males) from *ID* - 20 km N Malad City, 20 km N Rexburg, and 15 km W of Stone.

**Diagnosis**. This taxon resembles *M. strictus*, but has a distinctly sinuate aedeagal shaft. From typical *M. caprillus* it is most readily distinguished by the conical tip of the style. It is judged to be a subspecies of the prairie leafhopper *M. caprillus* based on four males taken along with two nymphs and 13 females at the summit of Lemhi Pass on the ID/MT border. Their male style is intermediate in form (Fig. 21).

**Remarks.** The subspecies appears to be restricted to the upper Snake River drainage basin of southeastern ID and northeastern UT. It is separated from the typical subspecies in southeastern UT by Daniels Pass (2500m) 27 km SSE of Heber City between the Uinta Mountains and the Monte Cristo Range. The typical subspecies southeast of the pass has a narrower style tip (Fig. 22A) than populations on the plains (Fig. 22B), suggesting character displacement at a time when the two closely related taxa were adjacent.

### ***Mocuellus caprillus strictus* stat.nov.**

*Mocuellus strictus* Ross and Hamilton, 1970*b*: 174.

**Diagnosis.** Subspecies *strictus* was previously considered to be a distinct species from the prairie-inhabiting *M. caprillus*, as they both occur in AB; but both taxa hybridize with subspecies *anfractus* (q.v.). Presumptive hybrids of *anfractus*× *strictus* from the upper Clark Fork valley in MT have the female pregenital segment with divergent instead of parallel-sided notches (compare in Ross and Hamilton 1970*b*, figs. 10, 12).

### ***Mocuellus quinquespinus* sp.nov.**

(Figs. 18 A-C)

**Etymology:** *quinque*, five; *spinus*, spine (noun in apposition); referring to the armature of the aedeagal tip.

**Adults**. Tawny with indefinite pale brown markings; crown weakly angled, as long as midline of pronotum, as in *M. larrimeri* (DeLong); genitalia as in typical *M. caprillus* (Ross & Hamilton 1970*b*, fig. 3B), but aedeagus shorter, in lateral aspect with wider tip and narrower socle (Fig. 18A), in ventral aspect with bulbous shaft and tip armed with an unpaired ventral tooth on the lip of the gonopore at the apical third of shaft, plus 2 pairs of divergent lateral processes, the longer pair directed caudad either side of rounded, transparent, apical knob (Fig. 18B); style short, tip with small, sharp preapical process (Fig. 18C). Length to tip of pygofer (omitting setae): male 3.4-3.5 mm, female 3.9 mm.

**Types**. Holotype male, **USA.** *UT*- [SE] Tabiona [0.9 mi S junction hwys. 35 and 208 along dry tributary of Duchesne R.], 11 June 1992 (K.G.A. Hamilton). Paratypes: 1 male, 2 females, same data as holotype. All types No. 22838 in CNCI.

**Additional material:** 2 females from *UT*- Ouray, 4 Aug. 1986 (R.F. Whitcomb) IPL 002506, and Zion National Park, 8 Aug. 1986 (R.F. Whitcomb) IPL 002561, both in CNCI. The first of these is 60 km E of the type-locality, but at a much lower elevation; the latter is in southwestern UT. Either or both may represent an undescribed species.

**Diagnosis**. The divergent apical processes are unique. The Palaearctic *M. ruthenicus* Emel'janov has similar male genitalia (Emel'janov 1962, figs. 84-85), but the apical processes are parallel rather than diverging, the aedeagal shaft is tubular rather than bulbous, and the unpaired ventral tooth on the lip of the gonopore lies at midlength of the shaft rather than at the apical third.

***Psammotettix diademata* sp.nov.**
(Figs. 26 A-B)
**Etymology:** *diadema*, an ornamented fillet, *-ta*, adjectival form; in reference to the wing pattern.

**Adults**. Grey with dark brown markings; head angled, as in *P. dentatus* Knull (Beirne 1956, fig. 453); tegmina 3 × as long as wide, in female marked with a circlet of 6 dark spots, in male with more extensive markings between veins as in *Hebecephalus occidentalis* Beamer & Tuthill (Beirne 1956, fig. 492); aedeagus in lateral aspect evenly curved and very narrow at base, ballooning to membranous apical half 3 × as wide as narrowest part of shaft (Fig. 26A), in caudal aspect strongly expanded on apical half beyond gonopore, deeply grooved on meson, shallowly notched at tip (Fig. 26B). Length: male 4.0 mm, female 4.2 mm.

**Types**. Holotype male, **CANADA.** *BC*- Queen Charlotte Islands (Graham I.), North Beach, halfway between Masset and Tow Hill 54°02'00"N 131°57'00"W, 19 Aug. 2001 (Allombewrt & Sylvain) GG-01-052, ENT001-008907. Paratypes: 2 females, same data as holotype, but ENT001-008897 and ENT001-008920. Holotype and paratype in Royal BC Museum; paratype No. 22839 in CNCI.

**Diagnosis.** This species has an angulate head like *P. dentatus*, from which it may be distinguished by the unusually bold markings and larger size. It is the most robust of the Nearctic *Psammotettix* (other species that are as elongate have narrower tegmina). Its male genitalia resemble those of *P. latipex* (Sanders & DeLong) (Beirne 1956, fig. 1204 "P. alienus"), but the gonopore lies further from the base and the shaft is narrower in lateral aspect. Other *Psammotettix* from the Old World that have a shaft with a narrow basal half and flared apical half have the tip pointed or rounded, not notched.

***Psammotettix greenei* nom.nov.**
*P. emarginatus* Greene, 1971: 25, preoccupied; nec Sawai Singh 1969: 356.
**Etymology:** patronym in honour of J.F. Greene, who first named this species.

**Remarks.** This is a species endemic to Oregon, and should not be confused with true *P. emarginatus* from India.

***Psammotettix nesiotus*** **sp.nov.**
(Figs. 27 A-B)
**Etymology:** *nesiotus* (noun in apposition), an islander.

**Adults**. Tan, head bluntly produced but not angled, tegmina 3 × as long as wide; similar to the abundant and ubiquitous *P. lividellus* (Zetterstedt) (Beirne 1956, figs. 456, 759, 1210), but aedeagus in lateral aspect evenly curved throughout length (Fig. 27A), in caudal aspect parallel-margined to tip (Fig. 27B), not narrowed beyond gonopore. Length: male 2.8-3.3 mm, female 3.0-3.5 mm.

**Types**. Holotype male, **CANADA.** *BC*- Bowser, [Vancouver I.], 20 June 1955 (G.E. Shewell). Paratypes: 15 males, 36 females, same data as holotype; 9 males, 4 females, Fanny Bay, V[ancouver] I., 20 July 1976 (K.G.A. Hamilton); 8 males, 5 females, Sea I., Vancouver [airport] (H.H. Ross) GL 458 on *Agrostis palustris*. All types No. 21874 in CNCI.

**Diagnosis**. As in dozens of other species in the genus *Psammotettix*, species characters are confined to details of the aedeagus. The evenly curved aedeagus of *nesiotus* is similar to that of *P. dentatus* Knull (Beirne 1956, fig. 1207), but lacks the toothed lateral margins. From the new-world *P. attenuens* (DeLong & Davidson) (Beirne 1956, fig. 1208) and the holarctic *P. lividellus* (including its possible synonym, *P. altimontanus* Mitjaev, 1969) it may be distinguished by the apical half of the aedeagus being a continuation of the shaft, and not a distinctly flattened process that is straighter than the shaft (Fig. 28A) or recurved. Other species in the genus do not have the aedeagal shaft arising at right angles from the socle.

**Remarks.** This species occurs on both sides of the Strait of Georgia. This species will probably be found in adjacent parts of Washington state.

### Genus *Sorhoanus* Ribaut, redefined

*Sorhoanus* Ribaut, 1946: 85. Type-species by original designation, *Cicada assimilis* Fallén, 1806.
*Boreotettix* Lindberg, 1952: 145, **syn.nov.** Type-species by original designation: *Cosmotettix serricauda* Kontkanen, 1949.
*Zelenius* Emel'janov, 1966: 129, **syn.nov.** Type-species by original designation, *Laevicephalus orientalis* DeLong & Davidson, 1935.

**Diagnosis.** A number of Nearctic species (Figs. 23-25) do not fit readily into European generic concepts that split *Sorhoanus* into a number of genera based solely on male genitalia (e.g., Ossiannilsson 1983). Thus, the genus in its broad sense (Oman 1949 and Beirne 1956, including species later assigned to *Boreotettix* Lindberg, *Lebradea* Remane and *Zelenius* Emel'janov) is preferred. This broad definition was expanded by Hamilton and Langor (1987) to include *Arthaldeus* Ribaut and *Lemellus* Oman. It is here restricted, by exclusion of *Lebradea* (q.v.), to those species having a combination of tenth segment undivided medially (Fig. 23B) and male pygofers with very long, dense brush of macrosetae extending from midlength. *Cosmotettix* Ribaut and *Hebecephalus* DeLong may have such setae, but their tenth segment is divided or only narrowly connected across the posterior margin.

***Sorhoanus involutus*** **sp.nov.**
(Figs. 23 A-E)
**Etymology:** *involutus*, rolled inwards; in reference to the unique pygofer margins.

**Adults.** Female unknown. Male unmarked yellow except for pale dashes either side of tip of right-angled crown, as in *S. pascuellus* (Fallén) (Beirne 1956, fig. 457), tegmina pale greenish and male abdomen black; male genitalia with pygofer tapered, dorsal edges inrolled and densely spiculate (Figs. 23A-B); tenth tergite longer than wide; internal genitalia similar to those of *S. debilis* (Uhler), but aedeagus shorter and stout (Fig. 23D), with inconspicuous dorsolateral spicules on shaft (Fig. 23E) and style tip blunter (Fig.23C). Length: male 3.6 mm.

**Types**. Holotype male, **USA.** *CO*- Marshall, nr Boulder, 12 June 1961 (C.H. Mann), swept from top of low mesa; No. 22840 in CNCI.

**Diagnosis**. The inrolled pygofer margin is unique.

***Sorhoanus virilis* sp.nov.**
(Figs. 24A-B, 29A)
**Etymology:** *virilis*, of the male; in reference to the large male pygofers.

**Adults.** Similar to *S. debilis* (Figs. 25A-C, 30A), with dorsum unmarked yellow, tegmina pale green, face brown with pale arcs, abdominal tergites of female and rest of body of male black, but tenth tergite and male pygofers much larger, the latter ending in truncate, coarsely serrate tips (Fig. 24A); aedeagus sinuate at base, serrate on both dorsal and ventral margins (Fig. 29A), style evenly curved and without serrations (Fig. 24B). Length: male 3.7-3.9 mm, female 4.3-4.6 mm.

**Types**. Holotype male, **USA.** *OR*- Siskiyou, 14 June 1959 (Kelton & Madge). Paratypes: 1 male, 2 females, same data as holotype. All types No. 22841 in CNCI.

**Diagnosis**. The long tenth tergite is similar to that of *S. involutus* (Fig. 23B), but these species are not closely related.

***Sorhoanus xiphosura* sp.nov.**
(Figs. 32A, 33A)
**Etymology:** *xiphos*, sword; *ura*, tail (noun in apposition); in reference to the long spine at the base of the aedeagus.

**Adults.** Similar to *S. uhleri* (Oman) (Beirne 1956, figs. 461, 764, 1214), with dorsum unmarked yellow, tegmina pale green, usually influscated on apical cells and sometimes between veins throughout, face brown (at least on margins) with pale arcs, abdominal tergites of female and rest of body of male black; genitalia as in *S. uhleri* (Figs. 34-35A), but aedeagal base sharply pointed, caudal margin not minutely serrate (Fig. 33A), and shaft often longer and more slender (Fig. 32A). Length: male 3.5-3.9 mm, female 4.0-4.5 mm.

**Types**. Holotype male, **USA.** *UT*- Smithfield, 30 May 1968 (G.F. Knowlton) GL 983-984. Paratypes: 6 nymphs, 27 males, 8 females, same data as holotype; 26 nymphs, 60 males, 75 females, 22 May-14 August, from **CANADA.** *BC*- Creston, Michael, Okanagan lakehead, Summerland; **USA.** *ID*- Arco, Ketcham, 32 km SW Lolo Hot Springs [MT], 20 km N of Malad City, 12 km SE Moyie Springs, 4 km N of New Meadows; *MT*- 9 km S of Libby, 18 km W of Ovando, 3 km W Potomoc, Wisdom; *OR*- Bend, Joseph and 11 km E; *UT*- Logan; *WA*- 4 km S Del Rio; *WY*- 13 km SE of Cooke City [MT]. All types No. 22842 in CNCI.

**Diagnosis**. Males with short aedeagal shafts resemble those of *S. uhleri*, but lack the minute serrations on the shaft, having instead a single sharp point on the anterior angle. Males with longer aedeagal shafts, as in *S. orientalis* (DeLong & Davidson) (Fig. 31A), are immediately distinguishable by the degree to which the aedeagal base is produced. Both *S. uhleri* and *S. xiphosura* differ from *S. orientalis* and other species in *Sorhoanus* in having the caudal third of the ventral connective fused into a common stem, instead of being a simple loop.

**Remarks.** Associated nymphs vary from entirely tan to greenish with black venters. This series may represent a mixture of species.

***Stenometopiellus vader* sp.nov.**
(Fig. 36A)
**Etymology:** *vader* (noun in apposition), wanderer; in reference to its disjunct distribution with respect to *S. cookei*.

**Adults**. Characters as in *S. cookei* (Gillette) (Beirne 1956, figs. 428, 1182), but head markings usually faint, female pregenital sternite with a slightly narrower median process, either with excavated sides and rounded tip, or with straight sides converging at approximately 60°, and aedeagus in lateral aspect most strongly curved near base, shorter by 0.1 mm (Fig. 36A). Length: male 2.2-2.3 mm, female 2.2-2.5 mm.

**Types**. Holotype male, **USA.** *ID*- 12 km N Leslie, 6 June 1992 (K.G.A. Hamilton) [ca. 2000 m ]. Paratypes: 1 male, 6 females, same data as holotype. All types No. 22843 in CNCI.

**Diagnosis.** The short, U-shaped aedeagus distinguishes this species from its congener (Fig. 37A). The female pregenital sternite has a narrower process than that of most specimens of *S. cookei* (which usually has a broadly rounded or blunt-tipped process with sides converging at approximately 90°).

**Remarks.** Some females not associated with males cannot be distinguished with certainty. For this reason, two females taken 8 km W of Anaconda, MT are not included in the type series of *S. vader* although they are probably conspecific.

***Unoka dramatica* sp.nov.**
(Fig. 1)
**Etymology:** *dramatica*, dramatic; in reference to its bold markings.

**Adults**. Characters as in *U. gillettei* Metcalf (Beirne 1956, figs. 505, 801, 1259), but more darkly patterned (Fig. 1): head including face and abdominal tergites black or blackish-rufous, as dark as pronotal and tegminal bands, face unmarked or with faintly indicated paler lines on frontal arcs, and gena sometimes marked with brown lines bordering clypellus or with genal lobes embrowned; legs deep crimson to black; scutellum with black band at base sometimes extending across half its length; tegminal bands broad, uninterrupted, at least as wide at costa as distance between them.

**Types**. Holotype male, **CANADA.** *BC*- Osoyoos L., Osoyoos IR 1, 49°04'N 119°29'W, 5-30 May 1994 (G.G.E. Scudder) pitfall trap P 3-2 [in] *Purshia* assoc. AN BGxh. Paratypes: 14 males, 8 females, 2 nymphs, same data as holotype, but various traps; 2 males, same locality, 6-31 May; 5 males, 13 females, same data, 30 May-4 July; 1 male, same data, 3 Oct. 1994 - 11 Apr. 1995; 7 males, 5 females, Inkaneep, Osoyoos IR 1, 49°09'N 119°32'W, 31 May-5 July

1994; 1 male, Mud L., Osoyoos IR 1, 49°13'N 119°31'W, 2 June-7 July 1994. Holotype and 29 paratypes No. 22844 in CNCI; 29 paratypes in University of British Columbia, Vancouver.

**Additional material:** 30 males, 15 females from **CANADA.** *BC*- Mt. Kobau 560 m , Oliver, Osoyoos, Vaseau Ck., Venables Vly. [50° 36'30" N 121° 20'0" W], 30 May, 3 and 23 June, 16 July, 14-17 Aug. and (female only) 2 Sept. Possibly two broods (May - 4 July, 16 July - 2 Sept.)

**Diagnosis.** This species is closely related to *U. gillettei*, but has more extensive dark markings and a darker head. The latter species usually has a rufous head, which in the darkest form has paler brown areas across the clypellus; the pronotal band as well as the abdominal tergites may also be paler than the tegminal bands; the tegminal bands are narrower than the white spaces between them (Fig. 2), and the median band is often broken into spots or obsolete between the costas.

**Biology.** According to G.G.E. Scudder (pers. comm.) the type-locality has much sand dropseed, *Sporobolus cryptandrus* (Torrey) A. Gray. This is probably its host, since the related *U. gillettei* is a specialist on this grass.

**Remarks.** This species is known from two widely separated localities in southern BC: the southern Okanagan Valley and the Fraser Valley south of Ashcroft.

## DELPHACIDAE

Delphacidae (Figs. 3, 38-60), in contrast to leafhoppers, exhibit considerable interspecific variation in head, body and leg proportions; their colour patterns are generally conservative within most genera or subgenera. The characteristic Delphacid "calcar" or hinged process at the apex of the hind tibia is an important but unused generic character. The higher classification of Nearctic Delphacidae is presently under revision, and keys to the Canadian fauna will become available in the near future. The following Delphacid taxa represent five redefined genera with one new synonymy, one genus reduced to subgenus, four new combinations, and nine new species.

***Achorotile apicata* sp.nov.**
(Figs. 38A-C)
**Etymology:** *apicata*, apical; in reference to the spiny tip of the aedeagal shaft.

**Adults**. Colour and form as in *A. acuta* Scudder (1963, figs. 1 a-c), but male anal process shorter, more strongly hooked (Fig. 38B); aedeagus straight nearly to tip, strongly constricted beyond midlength, apex with multiple rows of spicules, apical gonopore small and round (Figs. 38A, C). Length: brachypterous male 2.5 mm, female 2.5-2.9 mm; macropterous form unknown; width of crown between eyes 0.3 mm, of male pronotum 0.8 mm, of female 0.9 mm, slightly wider than head; length of face above clypellus 0.5-0.6 mm, of antenna 0.4 mm, with 2$^{nd}$ antennal segment subequal to calcar; medial length of fore tibia 0.6 mm, of hind tibia 0.7-0.8 mm, of hind tarsus 0.7 mm.

**Types**. Holotype male, **USA.** *UT*- Summit Co., 58 km S of Evanston (WY), 12 June 1992 (K.G.A. Hamilton). Paratypes, 2 males, 18 females, same data as holotype. All types No. 22845 in CNCI.

**Diagnosis**. This species is similar to *A. acuta*, but the male has longer legs (fore tibia 0.5 mm and hind tarsus 0.6 mm in *A. acuta*); the most striking genital character is the aedeagus with a distinctly shorter, more spiculate tip. Other species of *Achorotile* Fieber have the tip of the aedeagus bent ventrad or with a ventral process near midlength.

### Genus *Caenodelphax* Fennah, redefined

*Caenodelphax* Fennah, 1965:96. Type-species by original designation: *Liburnia teapae* Fowler, 1905.

**Diagnosis.** This genus with a tropical genotype and 10 Nearctic species (currently placed in *Delphacodes* Fieber) have males which combines a narrow crown and a black dorsum with contrastingly pale antennae. Their calcars are small and knife-shaped, as in the transcontinental pest species *Delphacodes campestris* (Van Duzee) and other wide-headed genera including *Eurybregma* and *Kosswigianella*. Other Delphacid genera with narrow crowns have large, foliaceous calcars. In some species of Nearctic *Caenodelphax* the face is unusually broad, convex and shining; these species may be sexually dimorphic, with females pale tan without contrasting antennae.

**Included species.** Included species. The only species that occurs in the PNW, *Caenodelphax atridorsum* (Beamer), comb. nov. from *Delphacodes*, is a dimorphic species with a wide face like that of *Caenodelphax nigriscutellatus* (Beamer) (see Bouchard et al., 2002). Other species in the genus occur in eastern and central North America and will be discussed in a later paper.

### Genus *Elachodelphax* Vilbaste, redefined

*Elachodelphax* Vilbaste, 1965: 14. Type-species by original designation: *Liburnia metcalfi* Kusnezov, 1929.

*Aschedelphax* Wilson, 1992: 89, **stat.nov.** (subgenus). Type-species by original designation: *A. hochae* Wilson, 1992.

**Diagnosis.** This Holarctic genus (with 1 Palaearctic species) is defined by the dark gena contrasting with the pale face, a character otherwise only known from tropical Delphacidae of the genus *Sogatodes* which have a much narrower crown. The gena is most strongly darkened in subgenus *Aschedelphax*. The styles are also usually short; but in other characters (e.g., foliaceous calcar shape) this genus resembles *Javasella* Fennah.

**Included species.** Five **new combinations** are created by this generic definition: *Elachodelphax* (s.s.) *indistinctus* (Crawford), *E. (Aschedelphax) bifida* (Beamer) and *Elachodelphax (Aschedelphax) pedaforma* (Beamer), all from *Delphacodes*, plus *E. (A.) coloradensis* (Beamer) and *E. (A.) hochae* (Wilson), both from *Aschedelphax*.

### *Elachodelphax* (*Aschedelphax) borealis* sp.nov.

(Figs. 40A, 51A)

**Etymology:** *borealis*, of the north wind.

**Adults**. Colour and form as in *A. hochae* Wilson (1992, figs. 62-66), but male pygofers smaller, not wider than preceding segment, tips bearing only one short hook (Fig. 51A) instead of two; styles when viewed edgewise narrow (as in Fig. 53A), but in widest aspect truncate with sharp, outwardly directed angles; aedeagus broad to midlength, then abruptly narrowed to half its width, straight nearly to rounded tip (Fig. 40A). Length: brachypterous male 2.3-2.9 mm, female 2.8-3.5 mm; macropterous male 4.3 mm, female 4.4-4.9 mm; width of crown between eyes 0.2 in male, 0.3 mm in female, of pronotum 0.8-0.9 mm, 0.1 mm wider than head; length of face above clypellus 0.6-0.7 mm, of antenna 0.3-0.4 mm, with 2nd antennal segment much shorter than calcar, entire antenna not more than 0.05 mm longer than calcar;

apical 2 segments of rostrum 0.35-0.4 mm; medial length of fore tibia 0.9 mm in male, 0.8 mm in female, of hind tibia 1.1 mm in male, 1.2 mm in female, of hind tarsus 0.9 mm in male, 0.8 mm in female.

**Types**. Holotype brachypterous male, **USA.** *NH*- Oakes Gulf, Mt. Washington 4700-5000' [1400-1500 m], 8 Aug. 1954 (Becker, Munroe & Mason). Paratypes, 3 brachypterous males, same data; 9 brachypterous males and 4 brachypterous females, same data, but 1 Aug.; 4 brachypterous males and 2 brachypterous males, same data, but 9 Aug.; 2 brachypterous males and 1 brachypterous female, Mt. Washington, 14 Aug. 1958 (J.R. Vockeroth); 1 brachypterous male, Mt. Washington 5000', 13 Aug. 1951 (G.S. Walley); 34 brachypterous males, 8 brachypterous and 8 macropterous females, *NY*- Whiteface Mt. 4600-4872', 19 July 1962 (J.R. Vockeroth); **CANADA.** *AB*- 1 brachypterous male each, Elkwater, 9 June 1956 (O. Peck) and Grande Prairie, 11 June 1951 (A.R. Brooks); *NF* (Labrador) - 1 brachypterous male and 6 brachypterous females, Goose Bay, 10-19 July 1978 (W.E. Beckel); 2 brachypterous males, 3 brachypterous females, Nutak, 26 July 1954 (E.E. Sterns); *QC*- 1 macropterous male, Forestville, 9 July 1950 (R. de Ruette); 2 brachypterous males, Mt. Lyall 1500' [450 m], 25 July 1933 (W.J. Brown); 2 brachypterous males, 3 brachypterous females, Parke Reserve, Kam. Co., 9 July 1957 (G.E. Shewell). All types No. 22846 in CNCI.

**Additional material.** Eleven brachypterous females (without associated males): 21 May-19 Sept., from **CANADA.** *NWT*- Bathurst Inlet; *ON*- Minnitaki; *SK*-Saskatoon.

**Diagnosis**. The styles are more obviously short and truncate than in any other species in the genus. This common and widespread Nearctic species appears to be related to *E. bifida* (from Arizona), but the styles are not bifid and the aedeagus is longer in proportion to its width, and does not have the tips turned dorsad.

### *Elachodelphax* (*Aschedelphax) mazama* sp.nov.

(Figs. 41A, 52A-B)

**Etymology:** *Mazama* (noun in apposition), a settlement northwest of the type-locality.

**Adults**. Colour and form as in *A. hochae* Wilson (1992, figs. 62-66), but male pygofers intermediate in size between that species and *A. borealis* (Fig. 52A); styles in widest aspect with fingerlike processes directed caudolaterad; aedeagus broad on basal third, then abruptly narrowed to half its width, straight nearly to rounded tip (Fig. 41A). Length: brachypterous male 2.6 mm, female 2.8-3.2 mm; macropterous form unknown; width of crown between eyes 0.3 mm, of pronotum 0.9-1.0 mm, 0.1 mm wider than head; length of face above clypellus 0.6 mm, of antenna 0.35 mm, with 2nd antennal segment much shorter than calcar, entire antenna 0.05 mm longer than calcar; apical 2 segments of rostrum 0.35-0.4 mm; medial length of fore tibia 0.9 mm in male, 0.8 mm in female, of hind tibia 1.1 mm, of hind tarsus 0.9 mm in both sexes.

**Types**. Holotype male, **USA.** *WA*- [4 km NW] Winthrop, [ca. 18 km SE Mazama], 10 June 1984 (K.G.A. Hamilton). Paratypes: 1 male, 4 females, same data as holotype. All types No. 22847 in CNCI.

**Diagnosis**. Although the series from WA is short, it shows consistent differences from the widespread *A. borealis*. The pronotum is 0.1 mm wider, the hind leg proportions of tibia to tarsus are identical in both sexes instead of being sexually dimorphic, the male genitalic capsule is 0.2 mm wider, the styles are more pointed (compare Fig. 52A to Fig. 51A) and the aedeagus has a longer tip beyond the wide base (compare Fig. 41A to Fig. 40A).

**Remarks.** These two species appear to be glacial-age disjuncts of a formerly transcontinental species.

***Elachodelphax* (*Aschedelphax*) *unita* sp.nov.**
(Figs. 42A, 53A-B)
**Etymology:** *Unita* (noun in apposition), a mountain range in UT.

**Adults**. Colour and form as in *A. borealis*, but male pygofers narrower in lateral aspect, sternal region oblique, producing apparent ventral extension in caudal aspect (Figs. 53A-B); styles fingerlike, directed dorsad; aedeagus tapered, somewhat narrowed at midlength, sinuate to pointed tip (Fig. 42A). Length: brachypterous male 2.4 mm, female 2.5-3.1 mm; macropterous form unknown; width of crown between eyes 0.2 mm in male, 0.3 mm in female, of pronotum 0.8 in male, 0.9 mm in female, 0.1 mm wider than head; length of face above clypellus 0.6 mm, of antenna 0.3 mm, with 2nd antennal segment much shorter than calcar, entire antenna 0.05 mm longer than calcar; apical 2 segments of rostrum 0.4-0.45 mm; medial length of fore tibia 0.7-0.8 mm, of hind tibia 0.9 mm in male, 1.0 mm in female, of hind tarsus 0.8 mm in both sexes.

**Types**. Holotype male, **USA.** *UT*- Cub Creek, Uinta [sic] Mts, 17 July 1952 (Bohart, Knowlton). Paratypes: 10 females, same data as holotype. All types No. 22848 in CNCI.

**Diagnosis**. The male genitalia are distinctive.

**Genus *Eurybregma* Scott, redefined**
*Eurybregma* Scott, 1875. Type-species by monotypy: *E. nigrolineata* Scott, 1875: 92.
**Diagnosis.** The North American species formerly included in *Eurysa* Fieber and later, tentatively placed in *Chilodelphax* Vilbaste (Wilson 1988), do not belong in either of these genera. *Chilodelphax* is only superficially similar to one of the Nearctic species in male genitalia, but the external characters (e.g., narrow crown) are quite different. *Eurysa* has a spotted face found in the new world fauna only in *Phyllodinus* Van Duzee and *Bakerella* Crawford. Nymphs of *Eurysa* have few abdominal pits (Ossiannilsson 1978), while nymphs of *Eurybregma* (including the Nearctic species) have characteristic rows of numerous abdominal pits (Anufriev 1987, fig. 3). This pit arrangement differs from those of *Achorotile* and *Laccocera* in having the most medially located pit removed at a greater distance than the others.

**Included species.** This data necessitates the removal of three North American species formerly in *Eurysa* to **new combinations**: *Eurybregma magnifrons* (Crawford), *Eurybregma montana* (Beamer) and *Eurybregma obesa* (Beamer).

***Eurybregma eurytion* sp.nov.**
(Figs. 43A, 44A-B, 54B)
**Etymology:** *eurys*, widespread; *-tion*, result; in reference to the ubiquity of this species in PNW grasslands wherever its sister species does not occur.

**Adults**. Colour and form as in *E. magnifrons* (Beamer 1952, fig. 2), but slightly narrower, head slightly narrower than pronotum in male, as wide as pronotum to slightly wider in female; anal process tiny; pygofer process inturned on upper margin (Fig. 54B); aedeagus straight nearly to tip, upper margin at tip sinuate (Fig. 44A) or (in southern morph, Fig. 43A) "kinked," lower margin spiculate, convex on apical third, apex serrate around apical gonopore (Figs. 43A, 44A-B). Length: brachypterous male 2.5-3.2 mm, female 2.7-3.5 mm; macropterous male 4.1-4.4 mm, female 4.2-4.7 mm; width of crown between eyes 0.3-0.4 mm, of head and pronotum 0.8-0.9 mm; length of face above clypellus 0.5-0.6 mm, of antenna 0.3 mm, with 2nd antennal segment subequal to calcar; apical 2 segments of rostrum 0.35-0.4 mm; medial length of fore tibia 0.7 mm, of hind tibia 0.8-1.0 mm, of hind tarsus 0.8 mm.

**Types**. Holotype male, **USA.** *ID*- 23 km SW Darlington, 7 June 1992 (K.G.A. Hamilton). Paratypes: 8 males, 10 females, same data as holotype; 1 male and 5 females, all macropterous, from *ID*- Mud Lake, 19 June 1984 (K.G.A. Hamilton) on *Agropyron*; 4 males, 2 females, all macropterous, *WA*- 9 km S of Methow, 10 June 1984 (K.G.A. Hamilton); 1 nymph, 38 brachypterous males and 41 brachypterous females, 1 macropterous male and 5 macropterous females, 25 May-19 June and 22 July, from **CANADA.** *BC*- 7 km W Douglas Lake, 5 mi W Hedley, Mission Flats [nr Kamloops], Princeton [airport]; **USA.** *ID*- 6 km S Baker, Galena Summit 2800m [S of Obsidian], 10 km E Howe, 12 km N Leslie, Lowman, and 37 km NE; *MT*- 5 km N Conner, Florence, Ketcham, 7 km W Lincoln, 8 km N Missoula, 18 km W Ovando, 15 km W Philipsburg, 6 km SE St. Regis; *OR*- Bend (Pilot Butte), 13 km E Joseph; *WA*- 5 km SW Chesaw, 7 km N Havillah, Orient, 12 km E Teanaway. All types No. 22849 in CNCI.

**Additional material.** Southern morph: 11 males and 8 females, all brachypterous, 8-13 June, from **USA**- *ID*: 20 km N Malad City; *UT*: 4 km SW Lakeside Resort, 7 km E Laketown. No associated males: 21 brachypterous females, 30 May-26 July, from **CANADA**- *BC*: Clinton, Jesmond, Osoyoos, Kamloops, 2 mi S Louis Creek, Venables Valley Rd. at Hwy. 97; **USA**- *ID*: Obsidian; *MT*: 8 km W Anaconda, Florence, 10 km N Three Forks, Cardwell; *WA*: 8 km S Grand Coulee.

**Diagnosis**. This species differs from *E. magnifrons* (Figs. 45A-B, 55B) in its stouter aedeagal shaft which is straight on the basal half, and in its inturned pygofer process. The ranges of typical *eurytion* and *magnifrons* abut at Princeton, BC without any sign of introgression.

### Genus *Kosswigianella* Wagner, redefined

*Kosswigianella* Wagner, 1963: 169. Type-species by original designation: *Delphax exigua* Boheman, 1847.

*Acanthodelphax* LeQuesne, 1964: 57, **syn.nov.** Type-species by original designation: *Delphax denticauda* Boheman, 1847.

**Diagnosis.** Spatulate antennae with the apical segment not more than twice as long as wide, and a contrastingly dark male abdomen, are synapomorphies linking the genera *Kosswigianella* Wagner and *Acanthodelphax* LeQuesne. A new species, described below, shows the close relationship between these taxa in having male genitalia combining the truncate pygofers and drop-shaped basal aedeagal attachment of *Kosswigianella* and ventral pygofer tooth of *Acanthodelphax*.

**Included species.** Synonymy of these genera creates **new combinations** for the species formerly in *Acanthodelphax*: the North American *K. analis* (Crawford) and 3 Palaearctic species, *K. denticauda* Boheman, *K. spinosus* (Fieber) and *K. transuralica* Anufriev.

### *Kosswigianella irrutilo* sp.nov.

(Figs. 3, 46A, 56A-B)

**Etymology:** *irrutilo*, become ruddy.

**Adults**. Redbrown, male (and sometimes female) abdomen deep chocolate brown. Head as wide as pronotum in male, slightly narrower in female; face above clypellus broad, 25% longer than wide, weakly inflated, smooth and shining with median carina scarcely evident; crown slightly wider than long in male, as long as wide in female; antenna short, 2nd segment spatulate as in *Kosswigianella exigua* (Boheman). Thorax with pronotal carinae short, curved outwards, ending near midlength of segment; brachypterous tegmina truncate, 25% longer than wide, covering only extreme base of abdomen, leaving 5 large abdominal segments exposed; hind tibia bearing two minute spines on outer edge; calcar small and knife-shaped. Male anal process strongly angled ventrad; genital ring with pygofers truncate, minute median process on venter (Fig. 56B); diaphragm transverse, with inturned upper edge; styles abruptly narrowed just beyond midlength, apices furcate (Fig. 56A); thecal ring drop-shaped, narrow upper end articulated between bases of anal tube; aedeagus lamellate, in lateral aspect sinuate with minute tooth near base and gonopore confined to narrowly rounded tip (Fig. 46A). Length: brachypterous male 1.6 mm, female 1.7-2.1 mm (only specimen of macropterous form with wing tips damaged); width of crown between eyes 0.3 mm, of head and pronotum 0.6 mm in male, 0.7 mm in female; length of face above clypellus 0.4 mm, of antenna 0.25-0.3 mm, with 2nd antennal segment subequal to calcar; apical 2 segments of rostrum 0.25-0.3 mm; medial length of fore tibia 0.3-0.35 mm, of hind tibia 0.5-0.55 mm, of hind tarsus 0.4-0.45 mm.

**Types**. Holotype brachypterous male, **USA.** *CO*- Tarryall, 17 June 1954 (H.H. Ross) GL 947. Paratypes: 1 brachypterous male, 180 brachypterous and 1 macropterous females, same data as holotype. All types No. 22850 in CNCI.

**Diagnosis**. The broad, shiny face, large anal processes, furcate styles and lamellate aedeagus are distinctive.

### *Kosswigianella wasatchi* sp.nov.

(Figs. 47A, 57A)
**Etymology:** *Wasatch* (patronym), a mountain range in UT.

**Adults**. Colour and form as in *K. analis* (Crawford) (Figs. 48A-B, 58A), but face above clypellus broader, 45% longer than wide, crown less strongly produced; diaphragm narrowed either side of broad, median process on dorsal edge, and bearing prominent "heel" between bases of styles (Fig. 57A); aedeagus as in *K. analis* (Fig. 48A), but longer and more slender (Fig. 47A). Length: brachypterous male 1.8-1.9 mm, female 2.3-2.4 mm; macropterous male unknown, female 3.2-3.3 mm; width of crown between eyes 0.2 mm in male, 0.25 mm female, of male pronotum 0.7 mm, of female 0.8 mm, 0.1 mm wider than head; length of face above clypellus 0.4 mm in male, 0.5 mm in female, of antenna 0.25 in male, 0.3 mm in female, with 2nd antennal segment subequal to calcar; apical 2 segments of rostrum 0.25-0.3 mm; medial length of fore tibia 0.4 mm in male, 0.5 mm in female, of hind tibia 0.7 mm in male, 0.8 mm in female, of hind tarsus 0.5 mm in male, 0.6 mm in female.

**Types**. Holotype male, **USA.** *UT*- 11 km SW of Scofield, 10 June 1992 (K.G.A. Hamilton). Paratypes, 1 male, 5 brachypterous females, 2 macropterous females, same data as holotype. All types No. 22851 in CNCI.

**Diagnosis**. This species is a sister-species of the transcontinental *K. analis*, from which it may be distinguished by the slender aedeagal shaft and differently shaped diaphragm.

***Nothodelphax venusta* (Beamer), comb.nov.**
*Delphacodes venusta* Beamer, 1948: 115.
This is a sister-species to *N. foveata*, the type-species of the genus.

**Genus *Paraliburnia* Jensen-Haarup, redefined**
*Paraliburnia* Jensen-Haarup, 1917: 2. Type-species by original designation: *P. jacobseni* Jensen-Haarup, 1917 [=*Delphax concolor* Fieber, 1866].
**Diagnosis.** This broad-headed genus has an unusually long rostrum (apical two joints together 0.55-0.7 mm, at rest extending at least to metatrochanters) and very large, foliaceous calcars similar to those of the narrow-headed genus *Megamelus* Fieber. New World species also have close-set arms of the forked median carina extending onto the face between the eyes, although the smoothness of the apex of the head in some individuals makes these carinae hard to distinguish.

**Included species.** There are two Palaearctic species (Nast 1972). One Nearctic species *Paraliburnia kilmani* (Van Duzee: *Liburnia*) **comb.nov.** is transferred from *Delphacodes*. Two new, related species are described below.

***Paraliburnia furcata* sp.nov.**
(Figs. 49A-B, 59A-B)
**Etymology:** *furcata*, forked; in reference to the styles.

**Adults**. Colour and form as in *P. kilmani* (Van Duzee) (Wilson 1992, figs. 125-127), but much larger; crown of head slightly wider than long in male; anal process more robust (Fig. 59B); diaphragm narrowed mesally and produced caudad; styles small, abruptly narrowed on apical third, appearing furcate (Fig. 59A); aedeagus unarmed, tip dorsoventrally flattened above subterminal gonopore (Figs. 49A-B). Length to tip of brachypterous tegmen 2.5 mm [estimated overall length 3.0 mm]; width of crown between eyes 0.3 mm, of head 0.9 mm, of pronotum 1.0 mm; length of face above clypellus 0.7 mm, of antenna 0.55 mm, with 2nd antennal segment one-third length of calcar; apical 2 segments of rostrum 0.7 mm; medial length of fore tibia 0.9 mm, of hind tibia 1.0 mm, of hind tarsus 0.5 mm; calcar 0.5 mm; macropterous form and female unknown.

**Type**. Holotype male, **CANADA.** *BC*- Quesnel, 12 June 1949 (G.J. Spencer); No. 22852 in CNCI.

**Diagnosis**. In size and genital characters this species is most similar to the European genotype, but the styles are short and appear furcate, and the aedeagus is unarmed.

***Paraliburnia lecartus* sp.nov.**
(Figs. 50A, 60A-B)
**Etymology:** *lecartus*, arm (noun in apposition); in reference to the shape of the aedeagal shaft.

**Adults**. Colour and form as in *P. kilmani* (Wilson 1992, figs. 125-127), but with head wider, crown slightly wider than long in male (as in *P. furcata*) and as wide as long in female; anal process smaller; pygofer strongly bowed outwards above lower margin (Fig. 60B); diaphragm weakly sclerotized; styles short, strongly tapered, divergent (Fig. 60A); aedeagus armlike in lateral aspect, tapered towards enlarged tip, with ventral margin straight, upper margin concave and serrate, sides bearing unequally aligned serrate rows in a spiral pattern, that of the right side being most dorsally situated near the tip, but more ventrally placed near the base (Fig. 50A); gonopore just below tip. Length: brachypterous male 2.3 mm, female 2.1mm; width of crown between eyes 0.25 mm, of head 0.75 mm, of pronotum 0.8 mm; length of face above clypellus 0.55 mm, of antenna 0.4 mm, with 2nd antennal segment slightly shorter than calcar; apical 2 segments of rostrum 0.7 mm; medial length of fore tibia 0.7 mm, of hind tibia 0.9-0.95 mm, of hind tarsus 0.4 mm; calcar 0.35 mm.

**Types**. Holotype male, **CANADA.** *BC*- Fort St. John, Peace River, 10 June 1959 (G.G.E. Scudder); paratype female, same data; both types No. 22853 in CNCI.

**Diagnosis**. No other species in this genus has as small a calcar. The spiral arrangement of aedeagal serrations is also unusual.

## ACKNOWLEDGEMENTS

This study is dedicated to the memory of H.H. Ross (1908-1978). It is the outcome of many years of leafhopper surveys by "Herb" and his students to document the leafhopper fauna of North American grasslands, with special focus on Rocky Mountain grasslands. The manuscript was reviewed by D. Lafontaine of AAFC, Ottawa.

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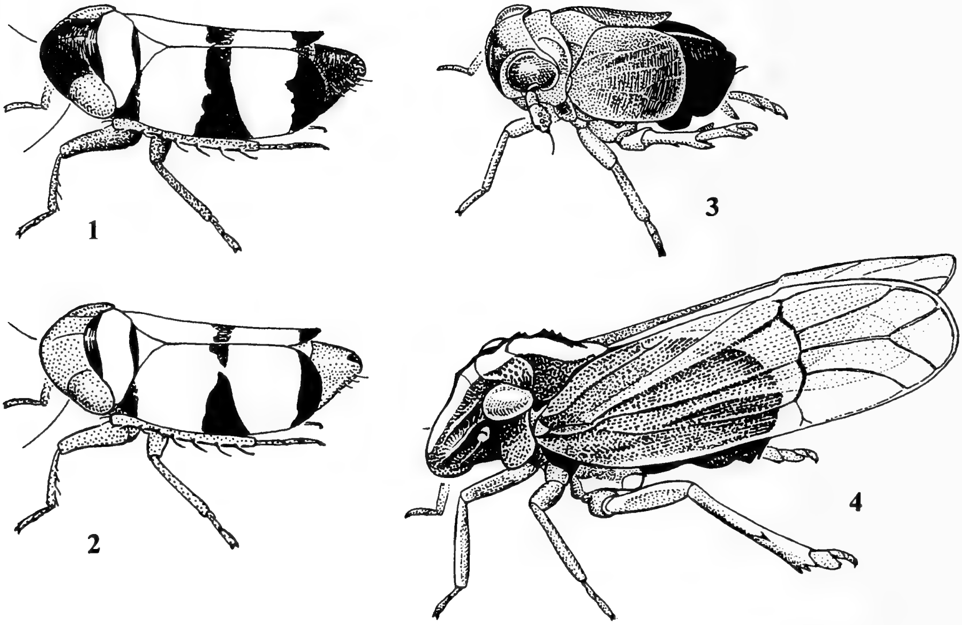
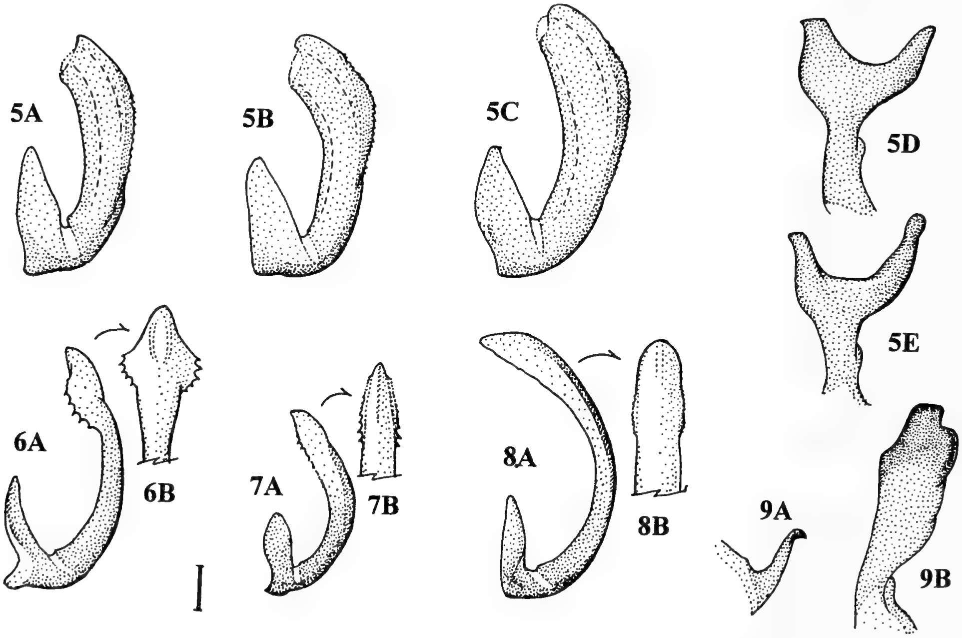
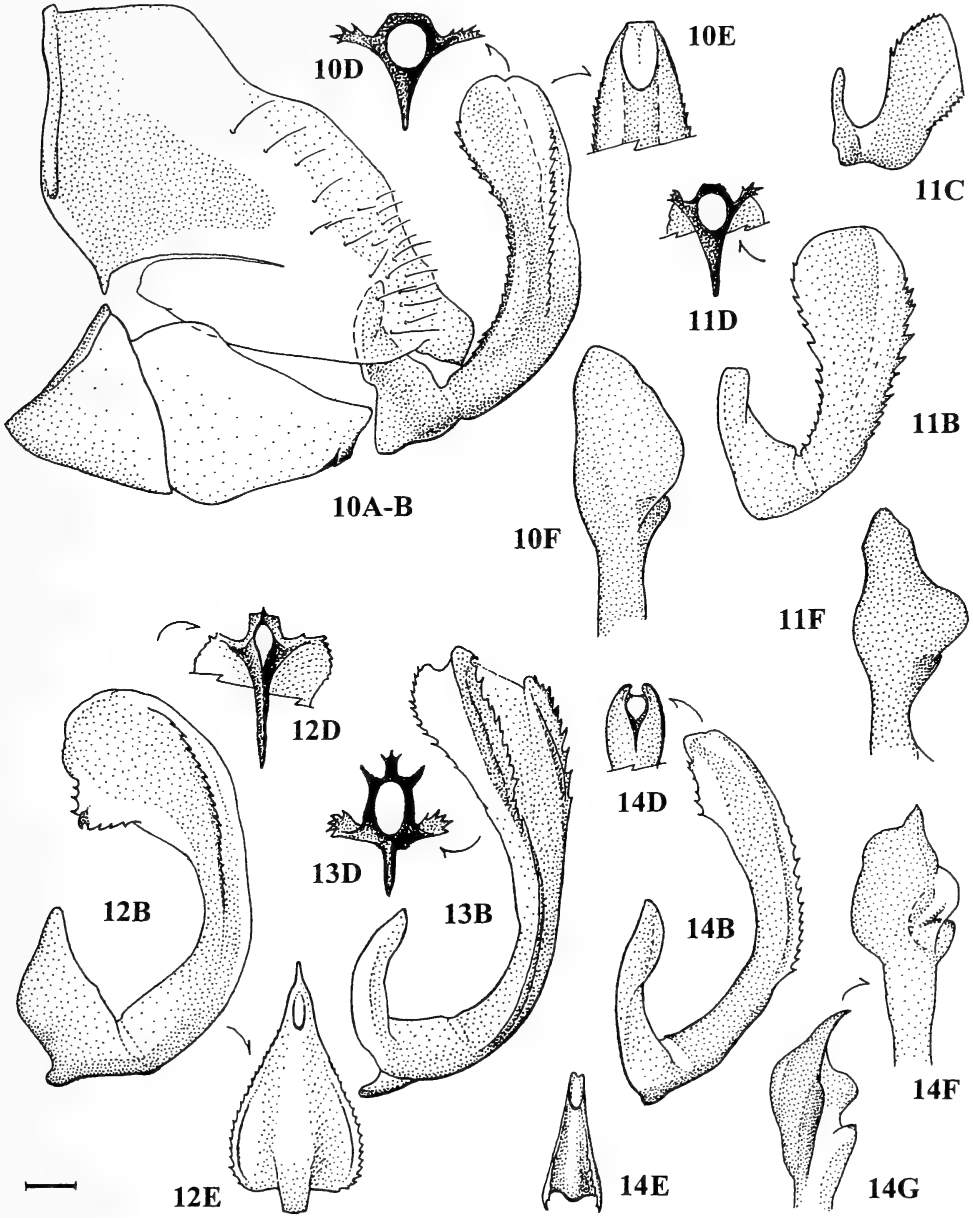


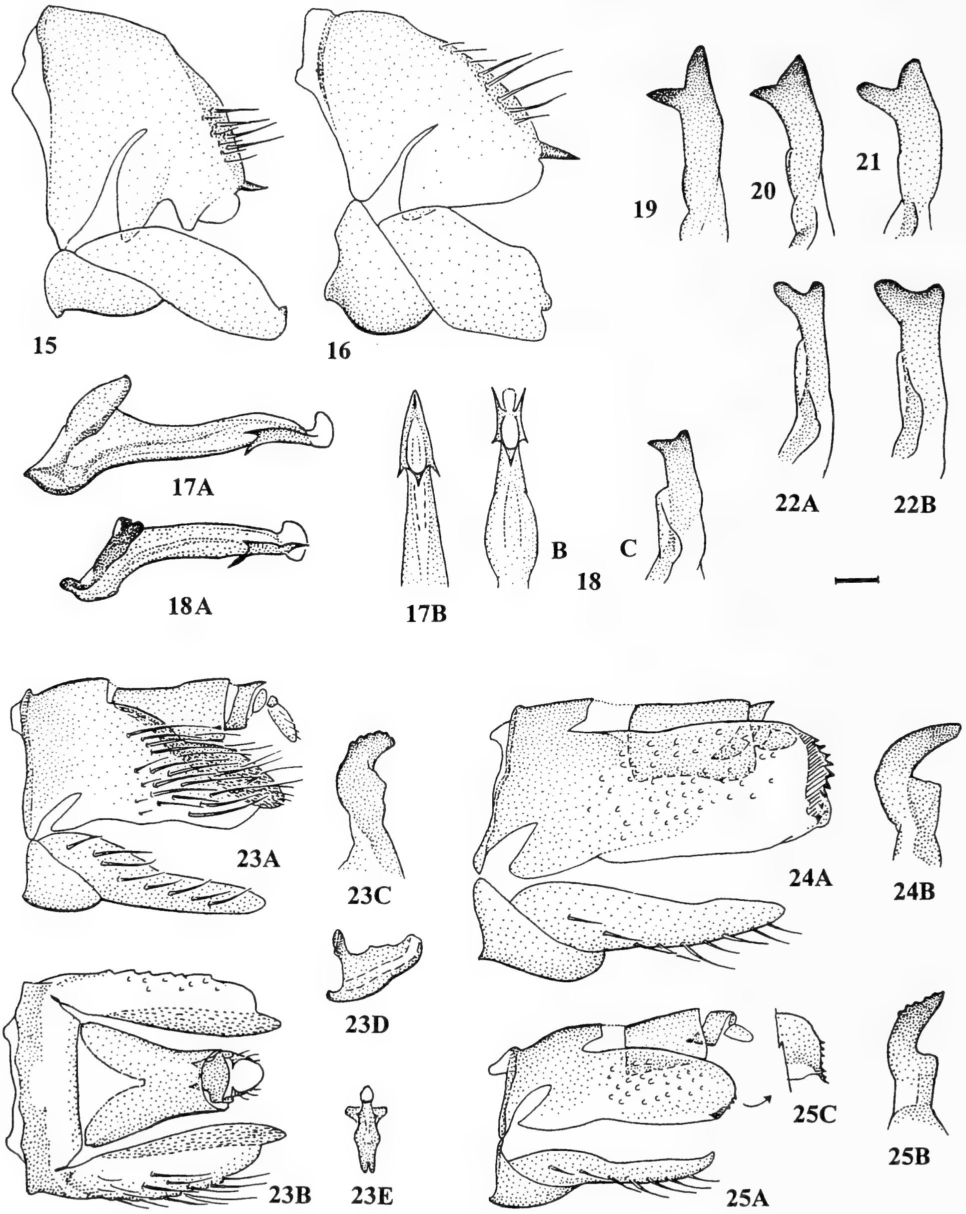
**Figures 1-4.** Homoptera-Auchenorrhyncha of PNW grasslands. 1, *Unoka dramatica*, palest form, Cicadellidae; 2, *Unoka gillettei*, darkest form; 3, *Kosswigianella irrutilo*, Delphacidae (brachypterous form); 4, *Bruchomorpha beameri*, Caliscelidae (macropterous form).



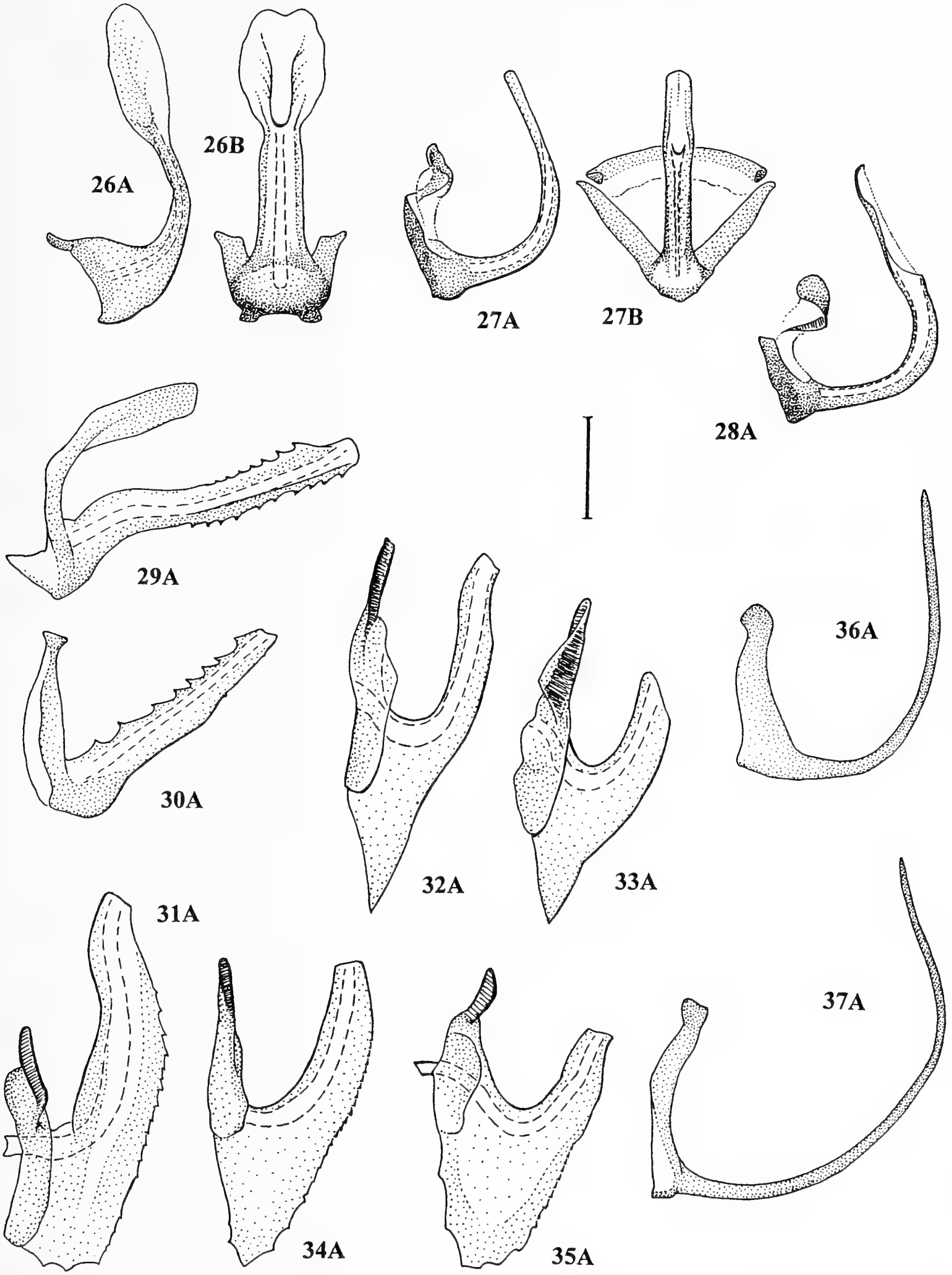
**Figures 5-9.** Male genitalia of Cicadellidae. 5, *Athysanella terebrans*, variation in lateral aspect of aedeagus (A-C) and distal part of style in widest aspect (D-E); 6, *A. occidentalis ladella*, lateral aspect of aedeagus (A) and tip of aedeagus in caudal aspect (B); 7, same, of *A. occidentalis* s.s.; 8, same, of *A. occidentalis megacauda*; 9, *A. hyperoche*, tip of pygofer (A) and distal part of style in widest aspect (B). Scale line: 0.1 mm.



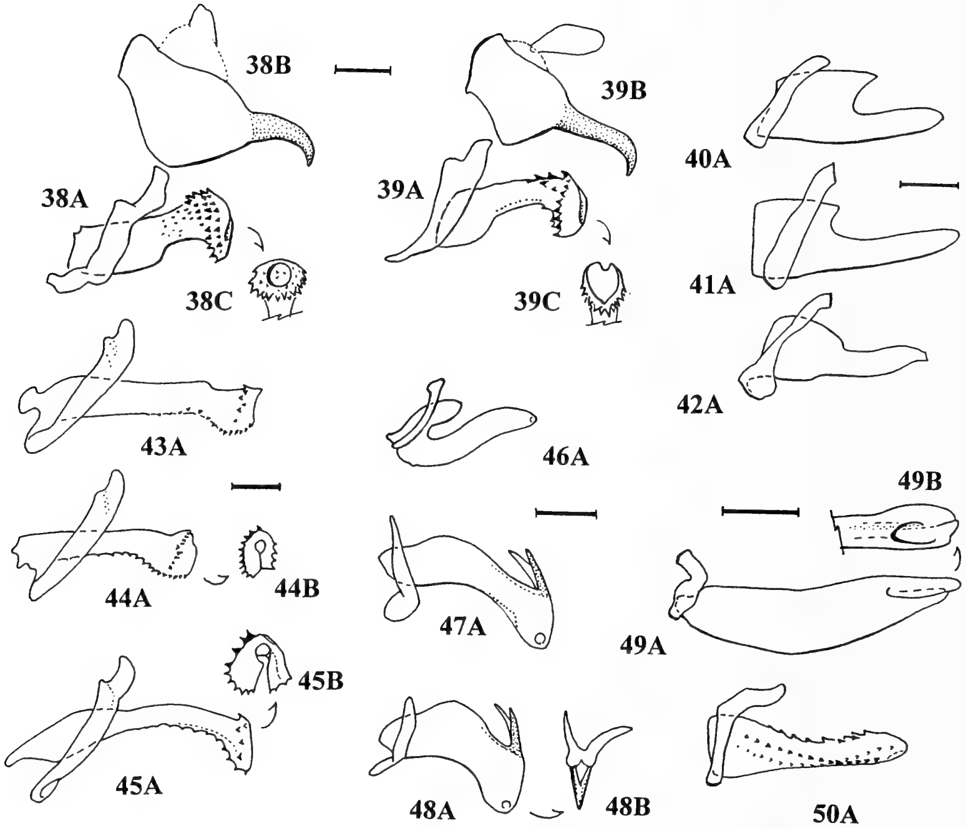
**Figures 10-14.** Male genitalia of Cicadellidae: genitalic capsule in lateral aspect (A), same, of aedeagus (B), same, parasitized individual (C), tip of aedeagus in dorsal aspect (D), same, in caudal aspect (E), distal part of style in widest aspect (F) and in narrowest aspect (G). 10(A-B, D-F), *Athysanella lemhi*; 11(B-D, F), *A. castor* ; 12(B, D-E), *A. expulsa*; 13(B, D), *A. attenuata*; 14(B, D-G), *A. repulsa*. Scale line: 0.1 mm.



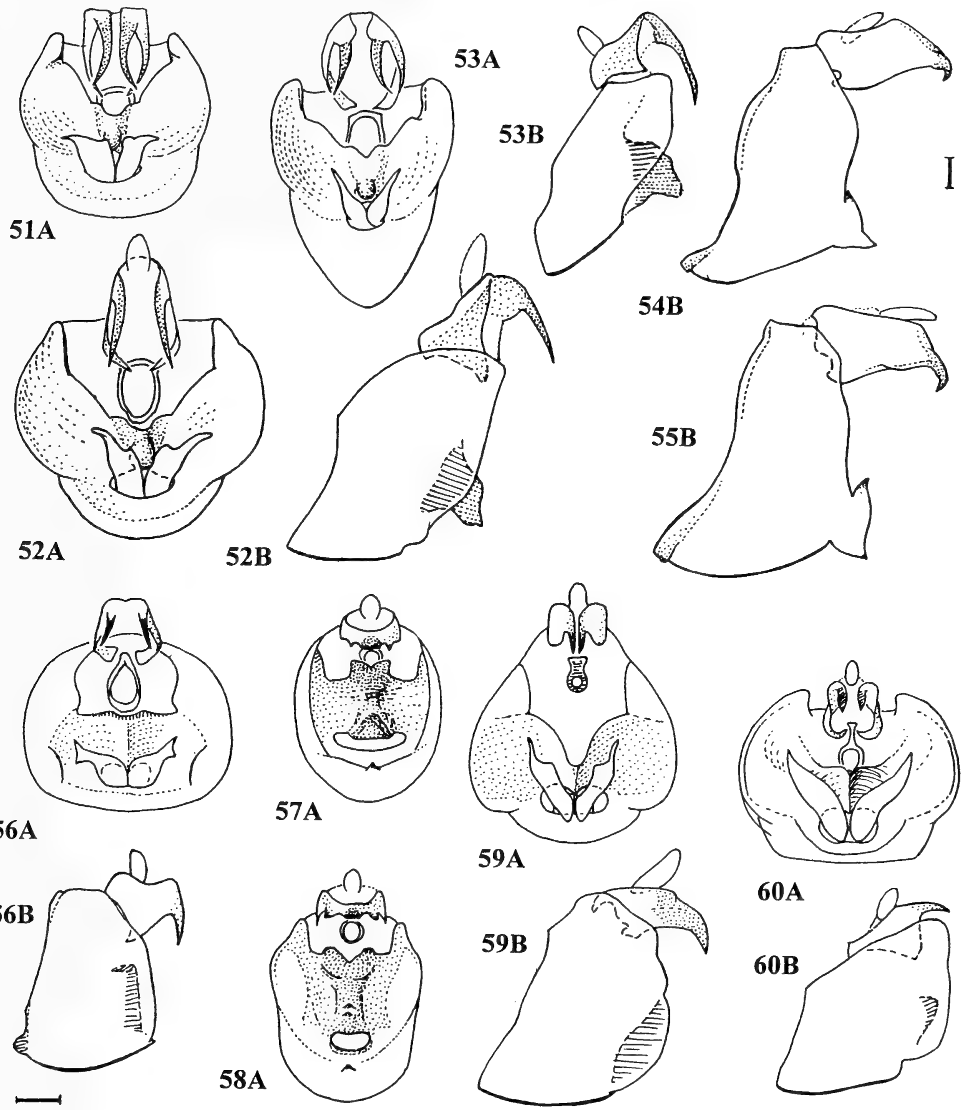
**Figures 15-25.** Male genitalia of Cicadellidae. 15, *Diplocolenus configuratus bicolor*, genitalic capsule in lateral aspect; 16, same, of *D. configuratus nigrior*; 17, *Mocuellus caprillus anfractus* aedeagus in lateral aspect (A) and in caudal aspect (B); 18, same, of *M. quinquespinus*, with distal part of style in widest aspect (C); 19, *M. caprillus strictus*, distal part of style in widest aspect ; 20, same, *M. caprillus anfractus*; 21, same, of *M. caprillus*□*anfractus* from Idaho/Montana border; 22, same, of *M. caprillus* s.s. from Utah (A) and from Alberta (B); 23, *Sorhoanus involutus*, genitalic capsule in lateral aspect (A), in dorsal aspect (B), distal part of style in widest aspect (C), aedeagus in lateral aspect (D) and in caudal aspect (E); 24, *S. virilis*, genitalic capsule in lateral aspect (A) omitting pygofer setae, and distal part of style in widest aspect (B); 25, same, in *S. debilis*, with detail of pygofer apex in ventrolateral aspect (C). Scale line: 0.1 mm..



**Figures 26-37.** Aedeagi of Cicadellidae, lateral aspect (A) and caudal aspect (B). 26, *Psammotettix diademata*; 27, *P. nesiotus*; 28, *P. lividellus*; 29, *Sorhoanus virilis*; 30, *S. debilis*; 31, *S. orientalis*; 32, *S. xiphosura*, holotype; 33. same, variety; 34-35, *S. uhleri*, varieties; 36, *Stenometopiellus vader*; 37, *Stenometopiellus cookei*. Scale line: 0.1 mm.



**Figures 38-50.** Male genitalia of Delphacidae: lateral aspect of aedeagal shaft (A), anal tube (B), and gonopore aspect of aedeagal shaft (C). 38, *Achorotile apicata*; 39, *A. acuta*; 40, *Elachodelphax borealis*; 41, *El. mazama*; 42, *El. unita*; 43, *Eurybregma eurytion* from Malad City, ID; 44, *Eu. eurytion*, smallest specimen from same locality as holotype; 45, same, of *Eu. magnifrons*; 46, *Kosswigianella irrutilo*; 47, *K. wasatchi*; 48, *K. analis*; 49, *Paraliburnia furcata*; 50, *P. lecartus*. Scale line: 0.1 mm, same scale for each genus.



**Figures 51-60.** Male genitalia of Delphacidae: caudal aspect of genitalia (A), omitting aedeagal shaft and (in Figs. 57-58), omitting small styles; lateral aspect of genital capsule and anal tube (B). 51, *Elachodelphax borealis*; 52, *El. mazama*; 53, *El. unita*; 54, *Eurybregma eurytion*; 55, *Eu. magnifrons*; 56, *Kosswigianella irrutilo*; 57, *K. wasatchi*; 58, *K. analis*; 59, *Paraliburnia furcata*; 60, *P. lecartus*. Scale line: 0.1 mm (Fig. 56A-B slightly larger).

# Homoptera (Insecta) in Pacific Northwest grasslands. Part 2 – Pleistocene refugia and postglacial dispersal of Cicadellidae, Delphacidae and Caliscelidae

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## ABSTRACT

Biogeographic analysis suggests that 241 Cicadellidae, 33 Delphacidae and 1 Caliscelid are restricted to grasslands in the Pacific Northwest. Nearly half of these (120 or 44%) are endemics. This grassland endemic fauna is third only to those of the prairies and desert grasslands. Of these, only six taxa probably postdate retreat of continental glaciers. The present distribution of the older taxa indicates that this fauna are descended from nine main glacial-era refugia (in descending order of importance): (1) east slopes of the Cascade Range, from Washington state to southern Oregon; (2) Columbia basin including Palouse hills of Washington and canyons of western Idaho; (3) south-facing slopes on the Rocky Mountains of Montana and western Wyoming; (4) the headwaters of the Snake River and south-facing slopes north of the Snake River in southern Idaho; (5) east of the Coast Range of Oregon; (6) edges of glacial Lake Missoula in western Montana; (7) a periglacial grassland near the ice front in Alberta; (8) the mountains of south-central Oregon; and (9) the coast of the Queen Charlotte Islands. Additional refugia might have been in the mountains of Colorado, Utah, eastern Arizona, and eastern Wyoming, where there are an additional 22 endemics. Postglacial warming brought grasslands and their endemic insects to British Columbia on the islands of the Strait of Georgia, to the East Kootenay valley and to the upper Fraser River of BC. Faunal exchanges have occurred across at least nine mountain passes on the continental divide. Three of these passes still provide continuous grassland connections between the prairies and the intermontane grasslands, yet not more than 14 slow-moving prairie species have surmounted any one pass.

## INTRODUCTION

Pacific Northwest grasslands, characterized in Part 1 of this study, are widely scattered across a largely mountainous landscape extending across six states and two provinces (Fig. 1). Specifically to the context of grasslands, Pacific Northwest (PNW) refers to the Great Basin and adjacent deserts, grasslands and open forests west of the continental divide extending from latitude 42° N both northwards and up slopes in mountainous areas to coniferous forests. This area encompasses all but the mountains of the states of Idaho (ID), Oregon (OR) and Washington (WA), plus the western parts of Montana (MT) and Wyoming (WY). Grassy intermontane valleys of southern and central British Columbia (BC) and on its coastal islands, plus foothills prairie of Alberta (AB) are also included in this faunal region. Similar grasslands extend southeast (Fig. 2) into the mountains of eastern Arizona (AZ), Colorado (CO) and Utah (UT). Low elevation grasslands of AZ, California (CA), western CO, Nevada (NV) New Mexico (NM) and UT are considered to be desert grasslands of the Great Basin and Sonoran subregions, or Mediterranean-zone shrublands.

PNW grasslands have undergone many vicissitudes during the last million years. Glaciers carved out most of the valleys in BC down into northern WA, ID and MT; other valleys in western MT have been inundated by glacial Lake Missoula as recently as 12,000 years ago;

and the Columbia Basin of WA has been repeatedly scoured by catastrophic floods emanating from glacial Lake Missoula (Waitt and Swanson 1987). It has been thought that, during the height of glaciation, tundra extended as far south on lowlands as WY and the Palouse hills of eastern WA, and in the mountains, as far south as southern CO and UT (Brunnschweiler 1962). Increased rainfall and colder temperatures also would have resulted in continuous spruce forest throughout the rest of the PNW. Such enormous changes in the PNW should have resulted in decimation of PNW grasslands by a combination of cool, wet weather and localized catastrophic events. That any fauna could survive appears almost incredible. Wholesale replacement of any grassland and its endemic insect fauna with widespread grassland species from southern refugia is the expected outcome. During the warmest postglacial period (the Hypsithermal) grasslands could have invaded the mountains from the prairies; but if so, grasslands must have been more extensive and less discontinuous in the PNW than at present.

It would seem unlikely therefore that PNW grasslands could ever have constituted a continuous, discrete ecozone. Yet many Homoptera are unique to these grasslands (for examples of new taxa, see Part 1 of this study). Furthermore, some are distributed relatively uniformly throughout the extent of the PNW. For example, *Texananus extremus* (Ball) not only ranges throughout the Cordilleran region, but is also found on the foothills prairie of southwestern AB. The purpose of this paper is to explore this paradox on the basis of evidence of recent insect distributions, and to deduce the factors responsible for this distinctive faunal assemblage. This study is the second detailed project emanating from a larger effort to study the leafhoppers endemic to North American grasslands, initiated by H.H. Ross in 1952. An overall summary was presented orally (Hamilton 1993) and a detailed study of the leafhopper fauna of the Yukon has been completed (Hamilton 1997).

Leafhoppers (Cicadellidae) are particularly important in characterizing native grasslands. They include the largest number of insect species endemic to the Great Plains (Ross 1970). There are more than 200 species endemic to prairies, and another 136 known only from desert grasslands, part of a total of some 800 grassland species in more than 80 genera (Hamilton and Whitcomb 1993). These insects contrast with other grassland arthropods such as spiders and ground beetles in being comparatively inefficient dispersers little influenced by microhabitat. Their dispersal rates are usually slower than 1 km/yr (Hamilton 1999*a*). Smaller numbers of Fulgoroidea (planthoppers) belonging to the families Delphacidae and Caliscelidae show similar endemism although (on limited data available) their dispersal appears to be more rapid than that of leafhoppers. Data are also available on grassland Delphacidae from the Yukon (Wilson 1997).

## METHODS

**Materials.** Ranges and host associations of Homoptera are based mainly upon surveys of PNW grasslands carried out by the author in July-August 1976, August 1978, June 1984, August 1985, May-June 1987, May-June 1992 and May 1995, which yielded samples of more than 57,000 specimens. Particular attention was focussed on 15 of the lowest Rocky Mountain passes between British Columbia and Wyoming (Table 1), plus adjacent grasslands at lower elevations. These records were supplemented by collections made by R.F. Whitcomb of USDA from 1977-1997 in most western states including MT, UT and WY, plus incidental records from the H.H. Ross "GL" (grassland) survey and other material in the Canadian National Collection of Insects (CNCI). Data from revisionary works (Lindsay 1940; Kramer 1971*a*; Johnson and Blocker 1979; Blocker and Johnson 1988, 1990; Hamilton and Zack 1999; Bartlett and Deitz 2000), and the only regional faunas, for WA (Wolfe 1955) and BC (Maw et al., 2000) are also cited; these represent thousands of additional specimens. Host records are those confirmed by my collecting, unless otherwise noted. For other recent revisions and taxonomic methodology, see Part 1.

**Table 1.**

Rocky Mountain passes sampled for Homoptera, BC to WY, lettered as in Figure 3. Omitted because not sampled: Deer Lodge Pass (1900 m), Elk Park, Flesher, Homesteak and Stemple passes in MT (2000 m), and on the ID/MT border, Reynolds and Red Rock passes (2100 m) and Bannack Pass (2300 m). Species numbered as in faunal list; hybrids (e.g., 14×87) are recorded for both parental populations.

| Pass | locale | elevation | direction | species in pass | species near pass | through pass? | total |
|---|---|---|---|---|---|---|---|
| "Crooked River" (A) | BC | 700 m | N/S |  | 27, 30 | 1, 8, 10, 14, 21, 50 | 8 |
| Yellowhead | BC/AB | 1200 m | E/W |  | 30 |  | 1 |
| Kicking Horse | BC | 1700 m | E/W |  | 13 |  | 1 |
| Crowsnest (B) | BC/AB | 1400 m | E/W |  | 9, 19, 26, 28, 51, 68 | 1, 2, 7, 10, 24 | 11 |
| Rogers (C) | MT | 1800 m | N/S | 1, 11, 16, 57, 50, 72 | 13, 20, 22, 31 | 28 | 11 |
| Lolo | MT/ID | 1800 m | N/S | 57, 67 | 74 |  | 3 |
| MacDonald (D) | MT | 2000 m | E/W | 13, 30, 57,68 | 7, 17, 72 | 51 | 8 |
| Pipestone | MT | 2000 m | N/S | 11, 67 |  | 24 | 4 |
| "Grassy" (E) | MT | 2100 m | N/S (open) | 28, 43, 73 | 3, 7, 13, 21, 22, 33, 38, 51, 53 | 4, 5 | 14 |
| Lost Trail (F) | ID/MT | 2100 m | N/S |  | 22, 43,68, 72 | 5, 32, 41, 57, 61, 69 | 10 |
| Chief Joseph | MT | 2200 m | E/W |  |  | 2, 12 | 2 |
| Lemhi (G) | ID/MT | 2200 m | E/W (open) | 3, 17×91, 36, 43, 72, 73 | 19, 31, 51, 83 | 32 | 12 |
| Bannock (H) | ID/MT | 2200 m | N/S (open) | 3, 22, 29, 36, 41, 43, 51, 53, 72, 73 | 87 | 4, 5, 22 | 14 |
| Monida (J) | ID/M | 2100 m | N/S (open) | 33, 34, 43, 57, 61 | 24, 51 | 6, 20 | 9 |
| Great Divide Basin (K) | WY | 2000 m | all (open) | 18 | 3, 17, 20, 23, 25 | 9, 15, 19, 21, 29, 31, 50 | 14 |

**Biogeography of Homoptera.** The PNW grassland fauna includes three introduced Eurasian species, the beet leafhopper *Neoaliturus (Circulifer) tenellus* (Zetterstedt), a sedge-feeding leafhopper *Euscelis obsoleta* (Kirschbaum), and the planthopper *Toya propinqua* (Fieber). They are excluded from this analysis because they were not part of the prehistorical fauna of the region.

As a first step in this biogeographic analysis, prehistorical patterns of endemism must be distinguished from stochastic patterns derived from rapid, opportunistic dispersal. For this reason, wind-dispersed "microleafhoppers" (Cicadellidae of the subfamily Typhlocybinae) are excluded from this biogeographic analysis. Other leafhoppers ("macroleafhoppers") include a few migratory species, of which only *Exitianus exitiosus* (Uhler) is a grassland species.

Planthoppers of the families Delphacidae and Caliscelidae also are used to determine whether the PNW fauna is essentially a prairie fauna, or an endemic intermontane fauna that survived glaciation. Slowest of all are "flightless" species of the genus *Errhomus* (although males can fly, their wingless females cannot have dispersed long distances: Hamilton and Zack 1999). Such insects are important in elucidating where glacial refugia could have been located.

Second, native grassland species must be distinguished from those with wider ranges. The former either feed exclusively on grasses, or are always associated with grassland sites provided that they do not feed on trees. In cases where their hosts are unknown, they are presumed to be similar to those of the most closely related species. This latter criterion is usually sufficient to distinguish tree-feeding species which are almost always in separate genera from those feeding on forbs and grasses. Many genera of leafhoppers and planthoppers feed exclusively on grasses, but this is a less reliable criterion since such genera often include sedge feeders of fens and bogs.

Almost all planthoppers of the families Delphacidae and Caliscelidae in the PNW are restricted to grasslands, with the exception of the rush and sedge-feeding Delphacid genera *Achorotile* Fieber, *Kelisia* Fieber, *Megamelus* Fieber, *Pentagramma* Van Duzee and *Stenocranus* Fieber, plus eleven common and widely dispersing species: one sedge-feeding Caliscelid, *Peltonotellus histrionicus* Stål; and ten Delphacids, *Delphacodes campestris* (Van Duzee), *D. consimilis* (Van Duzee), *D. lutulenta* (Van Duzee), *D. magna* (Crawford), *D. puella* (Van Duzee), *Javesella pellucida* (Fabricius), *Liburniella ornata* (Stål), *Phyllodinus nervatus* Van Duzee, *Pissonotus delicatus* Van Duzee and *Stobaera tricarinata* (Say).

The 38 leafhopper target genera are discussed in the first part of this project. Three genera are reported but not analysed here. *Ballana* (over 100 described species: DeLong 1964) needs revision. Preliminary analysis of this genus suggests that most of the species are confined to California and the Sonoran subregion, but that distribution patterns similar to those discussed below will be found in the PNW. The leafhopper genera *Deltocephalus* Burmeister (13 described species: Kramer 1971*b*) and *Draeculacephala* Ball (7 species complexes in northern North America: Hamilton 1985) present unresolved taxonomic and biological problems, with many (but not all) species restricted to sedge fens rather than to grasslands.

With these exceptions, the complete PNW fauna of "macro-leafhoppers" and planthoppers was examined to determine quantitative degrees of endemism, and to deduce dispersal rates. First, all native species of leafhoppers and planthoppers known from PNW grasslands were sorted according to their overall distribution patterns and known biology. Species that range into northern grasslands, prairies, or southern ("Great Basin" and "Sonoran subregion") grasslands are distinguished from those that appear to be truly endemic. Next, species that occur along the continental divide are individually analysed to determine whether dispersal patterns are discernible from present distributions. Finally, centres of endemism are compared for evidence of glacial-age refugia.

**Grassland characterization.** PNW grasslands are diverse, both geographically and botanically. The following is a synopsis drawn from many sources, including my own observations of areas sampled from surveys extending over seven years. For example, good collecting areas are usually found on south-facing slopes in Canada (Ross 1970) but farther south these become too arid. West-facing slopes are preferred by leafhoppers in the PNW.

For this analysis, PNW grasslands are assumed to be biologically similar to small (possibly relict) grasslands in areas outside the PNW, such as south-facing hillsides of the Yukon (Hamilton 1997). This study identifies such grasslands in the drier valleys of western and central British Columbia, and west-facing hillsides in the Rocky Mountains as far south as CO. These grasslands are subdivided into nine disjunct areas (Fig. 2 A-J), from west to east: (A) coastal areas of Pacific islands from the Queen Charlotte Islands (Fig. 2, star) of

northwestern BC, south to small islands in Puget Sound of northwestern WA;
(B) Pacific coastal grasslands, grassy "balds" on hills of the Coast Range, and valleys between the Coast and Cascade ranges of OR;
(C) the eastern slopes of the Cascade Range, from WA to the California border;
(D) the mountains of south-central OR;
(E) the Columbia basin including Palouse hills of WA-OR, adjacent canyons of western ID, and intermontane valley systems of central BC as far north as the Fraser River;
(F) the Snake River valley in southern ID and south-facing slopes north of the Snake River;
(G) the Upper Clark Fork valley system in western MT [for detailed analysis of dispersal patterns, subdivided into the smaller Blackfoot (Fig. 3, GA), Bitterroot (GB), and Rock Creek (GC) valleys];
(H) prairies east of the Continental Divide, from AB south to the Bighorn Mountains of northern WY; and
(J) a southward chain of high altitude grasslands in the mountains of eastern ID, western and southern WY, north-central CO, northern and central UT and eastern AZ.

Botanically, PNW grasslands form a complex of habitats (Munroe 1956; Küchler 1985; Ricketts et al. 1999) that are of four main types (Fig. 4):
(1) the largest area, extending from isolated valleys in BC south into WA and ID was originally Palouse prairie, dominated by mixed grasses generically similar to those on the prairies (Ecoregion 53 = Küchler zone 43);
(2) extensive sagebrush steppe (Ecoregion 75 = Küchler zone 49) has an ecotonal fringe of Palouse grasslands dominated in less arid areas by drought-hardy wheat grass (*Agropyron* spp.) and rice grass (*Oryzopsis* spp.);
(3) foothills prairie dominated with fescues (*Festuca* spp.) form a narrow altitudinal grassland on the eastern slopes of the Rocky Mountains (Ecoregion 57 = Küchler zone 56); and
(4) a limited area of oak savannah once occupied the Willamette Valley between the Coast Range and the Cascades (Ecoregion 6 = Küchler zone 24).

## RESULTS

Using admittedly subjective criteria, the Homopterous fauna of PNW grasslands, including adjacent montane grasslands, is calculated to consist of 215 species and 26 subspecies of "macro-leafhoppers" plus 34 species of planthoppers. This totals 275 taxa with a wide variety of dispersal characteristics (Faunal Synopsis and Index).

Species characteristic of boreal grasslands spread readily across mountain divides. There are 36 such leafhoppers that range as far north as the Yukon (Hamilton 1997) but only 17 leafhoppers and 4 planthoppers range from boreal grasslands into the PNW (Faunal Synopsis and Index). Their dispersal is stochastic; patterns are not discernible. They can be expected to occur wherever cool-season grasses are found.

Eight Delphacids and 50 leafhoppers are found in PNW grasslands southwards into CA and low elevations of AZ (Faunal Synopsis and Index). Some of these, notably *Orocastus tener* (Beamer & Tuthill) and *Psammotettix latipex* (DeLong & Davidson), range far into northern Canada (Hamilton 1997). These species most likely found a refugium in the southwest because north-south geographic barriers are minimal and summer winds bring flying insects such as migratory leafhoppers northwards from the Great Basin into western MT and southern BC (Carter 1927). All such planthoppers and all but 16 (65%) such leafhoppers have been found in Canada (Maw et al., 2000). By contrast, only one of four flightless southern leafhoppers migrated north to Canada. One of these, *Lystridea uhleri* (Baker), was able to cross the Columbia River only recently, almost certainly by human assistance (Hamilton and

Zack 1999).

More than 50 prairie species are widespread across the continental divide. There is no clear evidence for the direction of this spread, either onto the prairies from a montane refugium, or into intermontane grasslands from a prairie refuge. This fauna includes the only grassland Caliscelid in the PNW, *Bruchomorpha beameri* Doering, seven Delphacids, and 46 leafhoppers. Of these, 31 taxa range only a short distance into PNW grasslands. A comparison of their distributions may serve to indicate where the continental divide has been crossed recently and whether the territory available for colonization has been filled. Their dispersal routes are inferred on the assumption that the most direct routes are the ones that were actually taken.

This leaves 120 species and subspecies that are endemic to PNW grasslands plus 22 species which are endemic to montane grasslands adjacent to the PNW and are included for comparison. These together constitute 142 taxa endemic to grasslands of the PNW and adjacent mountains. Only six of these (Table 1, designated "?") are not known in sufficient detail to permit analysis.

The 136 well studied endemic taxa (114 from the PNW plus 22 from adjacent mountains) are compared to 25 prairie leafhoppers and six planthoppers that have limited distribution in the PNW. Their probable refugia and dispersal routes are discussed in three main faunistic sections.

First, the endemic taxa are divided into 130 ancient taxa and six subspecies which appear to be of postglacial origin. All six, belonging to the genus *Errhomus* (Hamilton and Zack 1999), either form local "swarms" of intermediate forms between adjacent, closely related species, or (in *E. truncus* Oman and *E. similis medialis* Oman) have unusual genitalic characters that appear to serve as distinguishing specific markers enhancing species barriers ("character displacement") where their ranges came in contact.

Next, 20 of the 130 taxa are considered to be glacial in origin since they have sibling taxa in adjacent areas, either separated by the continental divide, or occurring in isolated areas of the PNW. Taxa without close relatives, or ones whose ranges overlap, are considered to be preglacial in origin.

Finally, data from these 130 endemic taxa are synthesized for probable ecological distributions during the glacial period. They may or may not cross the continental divide, but have not invaded the prairies to any noticeable extent. Some are merely montane segregates of species that once were transcontinental; they now appear as pairs of sister taxa across the continental divide. Such species may have weathered Pleistocene glaciation in southerly locations, in which case their present distribution may show how they arrived where they now live. Other endemics represent pairs of sister taxa within the PNW, or as isolated species in small areas of the PNW that have no close relatives elsewhere. It seems reasonable to assume that these represent a fauna that survived the Pleistocene in intermontane valley refugia within, or close to, PNW grasslands. The location of these refugia may be traced most easily where modern distribution patterns are circular or elliptical, centred around a particular valley. Where this is not the case, it is assumed that the species has migrated northwards and/or to higher elevations in postglacial times, retreating from desertification to which it is not adapted.

## DISCUSSION

Three species that are characteristic of true prairies are aggressive dispersers, occurring in most suitable habitats: *Auridius auratus* (Gillette & Baker) (Hamilton 1999*b*, map 1), *Paraphlepsius lascivius* (Ball) (Hamilton 1975, map 9), and the planthopper *Laccocera lineata* Scudder (from the Fraser River of central BC southeast in PNW grasslands to the mountains of central UT, eastward to Saskatchewan, and found on the MT/ID border near

Rogers and "Grassy" passes, and in Bannock and Monida passes). Three species of *Hebecephalus* are also widespread (Hamilton 1998*a*), but their distribution in PNW grasslands is more erratic. All these species seem to be generalists on grasses. One other species, *Hardya dentata* (Osborn & Ball) from the prairies west to UT (being found just north of "Grassy Pass" and in Lemhi and Bannoch passes but not in the Snake River valley of ID), also has a "spotty" distribution in south-central BC and adjacent WA, and in OR east of the Cascade mountains. Still more disjunct are the known sites for two grass-feeding specialists of the leafhopper genus *Flexamia* DeLong (Whitcomb and Hicks 1988, figs. 30, 41). Since two-thirds of these species show disjunct distributions, the probability is great that some or all of these may represent the descendants of PNW relict populations of pre-glacial widespread ranges which have spread by opportunistic dispersal to other favourable sites.

Numerous species of the PNW appear to be endemic to the region. For example, of the 27 nearctic species of leafhoppers belonging to the genus *Hebecephalus*, 21 are endemic to the PNW and adjacent areas (Hamilton 1998*a*); and of the 47 taxa of the flightless leafhopper genus *Errhomus*, all but two are found exclusively in the PNW (Hamilton and Zack 1999). Only a few leafhoppers are widely dispersed throughout the PNW (Fig. 5).

The 140 PNW-endemic taxa analysed below show two major influences: (1) mountain chains, particularly the continental divide, which separate prairie-inhabiting species from those in PNW grasslands, and (2) glacial-era grassland refugia, which predetermined the subsequent dispersal and modern range of many PNW-endemic leafhoppers and planthoppers. The latter can be subdivided into refugia within the PNW, and those to the south of the PNW which may have contributed to the modern PNW fauna.

The most significant barrier between the eastern and western grasslands is the continental divide, which permits only limited faunal exchanges (Fig. 6, stars). A second barrier is formed by the Bitterroot Mountains along the northern half of the boundary between ID and MT. Although the latter is pierced by the Clark Fork River, this valley lies deep in the coniferous forest and is impassable to grassland flora and fauna. The only significant passes along this ridge north of the continental divide are at Lookout Pass (1400 m elevation), also deep in coniferous forest near Wallace, ID, and Lost Trail Pass (Fig. 6, F). An additional 21 main passes penetrate the continental divide between northern BC and the mountains of CO (Fig. 6, circles). Two of these passes do not have any official name. The one near Summit Lake on the Crooked River north of Prince George, BC is here referred to as "Crooked River Pass" to distinguish it from the better-known Summit Lake Pass in northern BC. The second, between Mt. Haggin and Grassy Mt. just south of Anaconda, MT is here called "Grassy Pass." The following faunal analysis details the evidence for 21 northern prairie leafhoppers and 3 planthoppers crossing the continental divide by way of these passes.

Species that penetrate the continental divide in CO or further southward, such as *Sorhoanus orientalis* (DeLong & Davidson), do not occur in PNW grasslands and are not included in this analysis.

Of the many species that are endemic to PNW grasslands, 14 pairs of sister taxa (16 leafhoppers, 10 planthoppers) occur on opposite sides of the continental divide. These sister-taxa appear to be of most recent origin, and might possibly be kept geographically separate by interspecific competition. Six taxa appear to be subspecies of postglacial origin. Another 28 species are widespread in the PNW but lack close relatives and are probably derived from preglacial stock; six of these occur as three pairs of sister-taxa in disjunct areas of the PNW. These PNW endemic faunas tend to have range extensions southeast into the mountains of CO, UT and WY. In addition, there are 22 endemic species that only occur in these areas marginal to the PNW: 12 in the mountains of CO and adjacent eastern WY (with two ranging north to southern MT), eight in the mountains of UT and adjacent western WY, and one (*Latalus histrionicus* Beirne) in the highest plateau of eastern AZ and also on Vancouver Island in BC.

The remaining 56 endemic species are limited to isolated parts of the PNW: 15 each in inland OR and in inland WA, 10 along the ID/MT border, six along the west coast of OR and WA, six in BC, and four in western MT, restricted to the upper reaches of the Clark Fork River and its tributaries (the basin of glacial Lake Missoula).

**Species crossing the continental divide.**

(A) CALISCELIDAE

1. *Bruchomorpha beameri* Doering is a planthopper of the northern prairies (records from southern Arizona and the Sacramento Valley of California [Doering 1940] must surely refer to other species) that is also found in many of the intermontane valleys of BC (Fraser, Okanagan and Kootenay rivers), northeastern WA (on the Pend Oreille River), and the Lake Missoula basin of MT. It seems to have been able to surmount both "Crooked River" and Crowsnest passes on the Alberta border, and has been taken in Rogers Pass, MT.

(B) CICADELLIDAE

2. *Amblysellus wyomus* Kramer is a leafhopper of the western prairies, a specialist on June grass, *Koeleria macrantha* (Ledeb.) Schultes [=*K. cristata* (L.) Pers.], that has been taken in the East Kootenay of southeastern BC and (Kramer 1971*a*) in the Bitterroot Valley of western MT. It has probably reached these sites across the continental divide by way of Crowsnest and Chief Joseph passes.

3. *Athysanella attenuata* Baker is a prairie leafhopper that feeds on wheatgrasses, *Agropyron* spp. It has been taken in both Lemhi and Bannock passes as well just north of "Grassy Pass" in MT (Fig. 7) and west of the Great Divide Basin in WY (Fig. 6 E, G, H, K). From these locations it has spread further west along both sides of the Snake River valley of ID.

4. *Athysanella obesa* Ball & Beamer is a grass-feeding prairie leafhopper that specializes on June grass. It is found east of the continental divide at Badger Pass (2000m elevation) west of Dillon, MT, and on the other side of the divide in the upper Snake River valley of eastern ID, on the Lost River Range due south of Bannock Pass (Fig. 6, H), and also in MT due west of "Grassy Pass" (Fig. 6, E) in Rock Creek valley.

5. *Athysanella robusta* Baker has the same range and grass host as *A. obesa*, but has not been taken in the upper Snake River valley. Its migration route was probably the same as that of *A. obesa*; neither is likely to have migrated from ID back into MT by way of Lost Trail Pass as neither species has been found in the Bitterroot valley.

6. *Athysanella terebrans* (Gillette & Baker) is a leafhopper of the prairies, a specialist on sand grass, *Calamovilfa longifolia* (Hook.) Schribn. which may have come to the upper Snake River drainage basin in eastern ID by way of Monida Pass. Four females have been taken at two sites.

7. *Auridius helvus* (DeLong), a June grass-feeding leafhopper of the western prairies and eastern "prairie peninsula" from Minnesota to Michigan, has invaded southeastern BC (probably through Crowsnest Pass) and the valleys of western MT (Hamilton 1999*b*, map 2) where it occurs in the headwaters of the Clark Fork River system. Populations have been found on either side of "Grassy" and MacDonald passes, suggesting multiple invasions across the continental divide. One population is found in Arizona near the Colorado River, and has probably come there in the same way as *Unoka gillettei* Metcalf (#25).

8. *Auridius ordinatus* (Ball), a grass-feeding leafhopper of the northern prairies ranging from the mountains of CO to isolated grasslands of Alaska (Hamilton 1999*b*, map 4) has invaded the upper Fraser valley of central BC by way of "Crooked River Pass."

9. *Ceratagallia arida* (Oman) is a polyphagous prairie leafhopper that crosses the

continental divide in southeastern BC near Crowsnest Pass (Fig. 6, B) and in southern ID, probably by way of the Great Divide Basin of WY (Hamilton 1998*b*, map 3).

10. *Ceratagallia viator* Hamilton is a northern prairie species with remote populations in the northwest and southwest (Hamilton 1998*b*, map 2). It has entered PNW grasslands only along the upper Fraser River and southeastern BC, probably by way of "Crooked River" and Crowsnest passes.

11. *Ceratagallia vulgaris* (Oman) is a polyphagous leafhopper that is widespread in eastern North America and also has populations on the far western plains including Rogers and Pipestone passes on the continental divide in MT (Hamilton 1998*b*, map 4).

12. *Flexamia decora* Beamer & Tuthill is a specialist on mat muhly, *Muhlenbergia richardsonis* (Trin.) Rydb. It is widespread on the prairies and has penetrated the continental divide at several places (Whitcomb and Hicks 1988, fig. 39). One population found in the Clark Fork valley, MT, probably came by way of Chief Joseph Pass, since other MT populations occur southeast of this pass. One population in Sublette Co., western WY, suggests that other populations in UT came there by surmounting the Great Basin divide.

13. *Diplocolenus c. configuratus* (Uhler) is the typical subspecies of a grass-feeding leafhopper of eastern North America that has crossed the continental divide on the ID/MT border at MacDonald Pass, probably also at Rogers and "Grassy" passes, and also at Bannock Pass (Fig. 8, open circles). Its tolerance of boreal conditions makes it the only prairie-inhabiting leafhopper that is known to have crossed Kicking Horse Pass between Banff and Yoho National Parks, having been found only 35 km west of the pass in BC. In more southerly passes it hybridizes with other subspecies (see # 83, 139 and Fig. 8, bull's-eyes).

14. *Elymana circius* Hamilton is a grass-feeding leafhopper of the Canadian prairies that also occurs in the Peace River district of AB and the upper Fraser River of central BC (Chiykowski and Hamilton 1985, fig. 8), probably by way of "Crooked River Pass," BC (Fig. 6, A).

15. *Idiodonus heidemanni* (Ball) is a leafhopper of the western plains as far north as MT that is also known from the upper Snake River in WY. It probably came there by way of the Great Divide Basin of WY. It is not the species recorded as "*Idiodonus heidemanni*" from CA (DeLong and Severin 1948) which is actually *Bonneyana schwartzi* (Ball).

16. *Mesamia ludovicia* Ball is a specialist on prairie sage, *Artemisia gnaphalodes* Nutt. (=*A. ludoviciana* Nutt.) that has been taken at Rogers Pass, MT.

17. *Mocuellus caprillus* Ross & Hamilton is a specialist on western wheatgrass, *Agropyron smithii* Rydb., that occurs throughout the grasslands of MT and WY, and southeast of the mountains of UT (Fig. 9). It has crossed the continental divide at least twice, probably at MacDonald Pass and Great Divide Basin, judging by the proximity to known sites for this species. It is also found at Lemhi Pass on the ID/MT border, where it hybridizes with *Mocuellus caprillus anfractus* (#88).

18. *Norvellina clarivida* (Van Duzee) is a specialist of *Atriplex* spp. in southern AB and SK, south in the mountains of CO and NM, and also occurs in UT (Lindsay 1940), having crossed Great Divide Basin at Creston, WY.

19. *Orocastus labeculus* (DeLong) is a northern prairie leafhopper feeding on spear grasses (*Stipa* spp.) It also has been found in southeastern BC (Cranbrook, Skookumchuck), eastern ID (Carmen) and the Unitas of northern UT (Duchesne) and therefore must have penetrated the continental divide in at least three places: Crowsnest, Lemhi and Great Divide Basin passes seem indicated. A short series containing only females and nymphs from south-central BC (Hedley) may prove to be an undescribed sister-species when males are found.

20. *Orocastus perpusillus* (Ball & DeLong) is an abundant northern prairie leafhopper feeding on spear grasses. It has penetrated the continental divide at two locations (Fig. 10): in the Lake Missoula valley and in the upper reaches of the Snake River. The most likely passes

it could have come through, considering its known range, are Rogers and Monida passes (Fig. 6, C, J). Its presence in western WY suggests that it has also crossed the Great Divide Basin.

21. *Pinumius sexmaculatus* (Gillette & Baker) is a grass-feeding leafhopper of the northwestern plains that also occurs along the Fraser River of central BC, just north of "Grassy Pass," MT, and on the foothills of the Unita Mountains of UT. The northern and southernmost populations west of the continental divide probably came there by way of "Crooked River Pass," BC and the Great Divide Basin of WY.

22. *Prairiana kansana* (Ball) is a prairie leafhopper that probably feeds on some woody plant. It has been found just west of Rogers Pass and just north of "Grassy Pass" in MT, in Bannock Pass and south of Lost Trail Pass in ID. As this species is not known from the Bitterroot valley of MT, it probably has approached Lost Trail Pass from the south, *via* Bannock Pass.

23. *Psammotettix totalus* (DeLong & Davidson) is a grass-feeding leafhopper of the northwestern plains from northern MT to WY that also occurs in the Snake River valley of south-central ID (DeLong and Davidson 1935), probably by way of the Great Divide Basin of WY (DeLong and Davidson 1935: "Cane Tree" and "Cattail Spring," WY are unknown localities).

24. *Rosenus cruciatus* (Osborn & Ball) is a leafhopper specialist on June grass that is widespread on the northern prairies including western MT. Populations throughout the Lake Missoula Basin and south of Monida Pass in ID probably are derived from the only one found to the east, on the upper reaches of the Missouri River. This would imply that the Lake Missoula Basin populations came through one or more of the many passes near Butte. From the dispersal patterns of other species, Pipestone Pass seems the most likely route. This leafhopper also occurs on the foothills of the Unita Mountains of UT, and in southern BC. Whether the southern populations arrived in UT from the Snake River plain of ID, or across the Great Divide Basin of WY, cannot be ascertained at present. The population in the East Kootenay of eastern BC must have come there through Crowsnest Pass. A female (incorrectly recorded as *Rosenus obliquus* by Maw et al. [2000]) taken at Kelowna, BC and a male from Myncaster (near the WA border) show that an isolated population also inhabits the Okanagan Valley. The source for this population is unknown; possibly it is a Hypsithermal relict.

25. *Unoka gillettei* Metcalf is a leafhopper specializing on sand dropseed, *Sporobolus cryptandrus* (Torr.) A. Gray, and ranging from southern Alberta and southwestern MT east to Minnesota and south to Colorado. It is also found on the same host in southwestern WY, UT and adjacent AZ and NV, and thus appears to have crossed the Great Divide Basin of WY (Fig. 6, K) and travelled down the Green River to the Grand Canyon (Fig. 6, stars). Populations in southern AZ are probably derived from a more southerly pass, as this species specializes on gyp dropseed, *Sporobolus nealeyii* Vasey from TX to AZ.

## (C) DELPHACIDAE

26. *Elachodelphax pedaforma* (Beamer) is a planthopper of the northern plains that also occurs just beyond Crowsnest Pass at Fernie, BC.

27. *Eurybregma magnifrons* (Crawford) is a prairie planthopper that has invaded the upper reaches of the Fraser River in central BC via "Crooked River Pass," and migrated as far north as Alaska, but has not crossed more southerly passes (Fig. 11).

28. *Laccocera canadensis* Beirne is a planthopper of the northern plains that also occurs in the East Kootenay valley, BC, and in MT along Rock Creek and the Blackfoot River in Lake Missoula Basin, and on "Grassy Pass." The population in eastern BC must have come there through Crowsnest Pass, while that on Rock Creek came by way of "Grassy Pass" and the lower pass at Silver Lake just to the west. The population on the Blackfoot River probably came there by way of Rogers Pass.

29. *Laccocera flava* Crawford is a northern prairie planthopper that has entered the headwaters of the Snake River of ID (Fig. 12, filled circles) by way of UT, probably traversing the Great Divide Basin of WY, and is also in the Lake Missoula valley of MT. Whether it came to the latter by way of MacDonald or by "Grassy Pass" cannot be determined. Its presence in both Bitterroot and Rock Creek valleys suggests that it was once widespread in the headwaters of the Clark Fork River. Its range may have become fragmented during the formation of glacial Lake Missoula. It also reaches the continental divide at Bannock Pass.

30. *Laccocera vittipennis* Van Duzee is a common polyphagous planthopper of northern prairies and Peace River grasslands on the western half of the continent, although not confined to grasslands in eastern North America. It has been found in BC just beyond "Crooked River" and Yellowhead passes, in MacDonald Pass and west of the pass in the upper reaches of the Lake Missoula valley (Fig. 13).

31. *Nothodelphax foveatus* (Van Duzee) is a common planthopper of northern prairie including the Peace River district. It also has been found in ID (the Lemhi Valley and in the upper Snake River plain), MT (Blackfoot River Valley), OR (shore of the Columbia River) and UT (foothills of Unita Mountains). Possibly it crossed the continental divide by way of Rogers, Lemhi and Great Divide Basin passes; from the Snake River plain it has invaded the Columbia River near its junction with the Snake.

## Pairs of sister taxa separated by the continental divide.

### (A) CICADELLIDAE

32. *Athysanella occidentalis megacauda* Hamilton (see Part 1) is a grass-feeding prairie leafhopper known only from southern interior of BC and northern WA, south along the Columbia as far as Vantage, WA. It was probably restricted to the Columbia canyon during the Pleistocene. Typical *occidentalis* occurs only east of the continental divide. A short distance to the west of the continental divide from the Bitterroot Valley of MT, south through the headwaters of the Salmon River and the Camas valley in ID occur a hybrid swarm between these two subspecies. To attain this distribution these hybrids must have crossed Lost Trail Pass and the still higher Galena Summit (2700m elevation) between the headwaters of the Salmon and Camas rivers. How typical *occidentalis* came across the continental divide is not known, but the most likely route is through Lemhi Pass (Fig. 6, G) which lies halfway between the extremes of its distribution to the west of the divide.

33. *Attenuipyga (Dorycara) minor* subspecies *setosa* Oman is a grass-feeding leafhopper known from widely scattered PNW grasslands of central OR and adjacent WA, southern BC, and the upper Snake River plain in ID. Its related subspecies, typical *A. minor* (Osborn), is entirely east of the continental divide. Individuals that appear to be hybrids between these subspecies have been taken just north of "Grassy Pass" in MT, and (Oman 1985) on the upper Snake River plain not far from Monida Pass, in the mountains of CO and northern UT, and central NV.

34. *Auridius ordinatus* subspecies *crocatus* Hamilton, a grass-feeding leafhopper, occurs throughout PNW grasslands and as far south as northern NV (Hamilton 1999*b*, map 4). It was probably widespread in PNW grasslands during the Pleistocene. It has two related geographical subspecies: typical *A. ordinatus* Ball (#8), a northern prairie subspecies, and subspecies *amarillo* Hamilton in the mountains of NM. Hybrids between the typical subspecies and *crocatus* are found at Monida Pass and adjacent areas of the upper Snake River valley.

35. *Ceratagallia nanella* subspecies *zacki* Hamilton, a polyphagous leafhopper in WA and southernmost BC (Hamilton 1998*b*, map 9), is related to two widely disjunct geographical subspecies: typical *C. nanella* Oman of the prairies and southwestern grasslands from Canada to AZ, and subspecies *australis* Hamilton in the mountains of Mexico. Subspecies *zacki* was probably widespread on the Columbia basin during the Pleistocene.

36. *Ceratagallia siccifolia* subspecies *compressa* Hamilton, a polyphagous leafhopper widespread in PNW grasslands, is related to two geographical subspecies: the widely disjunct subspecies *alaskana* Hamilton in the far northwest, and typical *C. siccifolia* (Uhler) which is mainly a prairie subspecies. Because the typical subspecies is widespread and aggressive, having been taken at Bannock and Lemhi passes, and up to 3300 m elevation in CO, it is assumed here to have been able to traverse all the mountain passes. It appears to have invaded the PNW before postglacial times. Its populations have completely swamped the PNW subspecies at higher elevations. Subspecies *compressa* is now confined mostly to valley bottoms (Hamilton 1998*b*, map 10).

37. *Psammotettix beirnei* Greene is a grass-feeding leafhopper known only from 7600' [2500 m elevation] on Mt. Harry in the Selkirk Mountains near Revelstoke, BC, erroneously recorded from Northwest Territories (Greene 1971). Its sister-species, *P. alexanderi* Greene is known only from the White Mountains of New Hampshire (Greene 1971).

38. *Stenometopiellus vader* Hamilton (see Part 1) has a sister species *S. cookei* (Gillette) on the northern prairies and mountains of CO. Both are sedge-feeding leafhoppers, the former at present known only from the Lost River Range of eastern ID and just north of "Grassy Pass" in MT. Its glacial-age refugium was probably the upper Snake River valley. Whether it spread to southern MT by way of Lemhi or Bannock pass and later entered the Lake Missoula basin by way of "Grassy Pass", or whether it invaded the Lake Missoula basin directly by way of Lost Trail Pass, cannot be determined at present.

39. *Unoka dramatica* Hamilton (see Part 1) is known only from southern BC (Fig. 6, filled circle) widely disjunct from its sister species *U. gillettei* (#25). This PNW endemic of sandy areas probably survived the Pleistocene in the upper reaches of the Columbia basin on sandy outwashes from terminal moraines.

### (B) DELPHACIDAE

40. *Elachodelphax mazama* Hamilton (see Part 1) is known only from the Methow Valley in northwestern WA. Its presence near the arid inland valleys of southern BC suggest that its parent species was once widespread throughout central BC. Its sister species is *E. borealis* Hamilton (see Part 1), a planthopper widespread from coastal Labrador and high mountains of New Hampshire west to the Peace River district of Alberta that is not known to have penetrated the Rocky Mountains.

41. *Eurybregma eurytion* Hamilton (see Part 1) includes in its extensive PNW range the Lake Missoula valley in MT, indicating that it must have surmounted Lost Trail Pass, as it has Bannock Pass (Fig. 11). It was probably widespread in PNW grasslands during the Pleistocene. Its sister-species, the prairie-inhabiting *E. magnifrons* (#27) is found north of the range of *E. eurytion*, except where they co-occur at Princeton, BC.

42. *Laccocera oregonensis* Penner has a disjunct distribution, in eastern ID and around the Columbia basin from southern BC to OR (Fig. 12, open circles). This suggests that it was probably widespread in PNW grasslands during the Pleistocene. Its sister species, *L. flava* (#29), may be inhibited in its westward spread by *L. oregonensis* just west of Lemhi Pass.

43. *Laccocera vanduzeei* Penner, sister species to *Laccocera vittipennis* (#30), is widespread from central BC to ID, and has many populations in the mountains of AZ, CO and UT (Fig. 13, open circles) where it probably found glacial refugia. It occupies the southern part of the Lake Missoula valley as well as the headwaters of the Missouri River in MT. It has been found in "Grassy", Lemhi, Bannock and Monida passes and adjacent to Lost Trail Pass. Multiple crossings of the continental divide seem indicated.

44. *Nothodelphax venustus* (Beamer), sister species to *N. foveatus* (#31), is confined to the mountains of southern BC and adjacent WA, southern WY and adjacent CO, and northern AZ.

**Endemic pairs of sister taxa in PNW** (CICADELLIDAE only).

45. *Athysanella expulsa* Blocker is a grass-feeding leafhopper known only from central OR east of the Cascade Mts. (Blocker and Johnson 1990).

46. *Athysanella repulsa* Hamilton (see Part 1), sister-species to *A. expulsa*, is known only from Flint Creek on the upper reaches of the Clark Fork valley of MT.

47. *Auridius cosmeticus* Hamilton (Hamilton 1999*b*, map 3) is a sedge-feeding leafhopper found only in the upper reaches of the Blackfoot and Bitterroot valleys of MT, where it seems to have found a refugium from the waters of glacial Lake Missoula.

48. *Auridius vitellinus* Hamilton, sister species to *A. cosmeticus* (Hamilton 1999*b*), is known only from southernmost OR east of the Cascade Mts.

49. *Latalus histrionicus* Beirne is known only from Vancouver Island, BC, and the high plateau of eastern AZ. Its range appears to reflect two isolated glacial-age refugia rather than competition with its sister-species (see #50), because both species can be found near Alpine, AZ.

50. *Latalus intermedius* Ross & Hamilton is a common grass-feeding leafhopper of mountains in eastern AZ, CO, UT and western WY (which were probably its glacial-age refugia). It has also established colonies in southeastern ID near the UT border, and at Rogers Pass, MT, and three sites in the north: Peace River district of AB and BC, on the upper Fraser River of central BC, and at Norman Wells on the Mackenzie River, Northwest Territories. It must have spread from central BC through "Crooked River Pass" to reach the Peace and Mackenzie rivers, and across the Great Divide Basin to reach UT and ID.

51. *Sorhoanus debilis* (Uhler) is a grass-feeding leafhopper from the eastern foothills of the Cascade Mountains from northern OR to intermontane valleys of southern BC and ID, and the mountains of central UT, eastern WY and CO (Fig. 14), all of which may have provided glacial refugia. It has crossed the Crowsnest Pass to Watertown, AB, and has invaded the headwaters of the Missouri River in MT by way of Bannock Pass and possibly also Lemhi and Monida passes. From the vicinity of Helena it may have crossed MacDonald Pass to establish a colony on the headwaters of the Clark Fork River; possibly it also crossed "Grassy Pass".

52. *Sorhoanus virilis* Hamilton (see Part 1), sister species to *S. debilis*, is known only from the Cascade Mountains of southernmost OR.

**Endemics without close relatives, widespread in PNW.**

(A) CICADELLIDAE

53. *Attenuipyga (Dorycara) omanae* (Beamer) is a leafhopper specialist on bluebunch fescue, *Festuca idahoensis* Elmer in widely scattered PNW grasslands from southern BC south to the highlands of central OR, east to Bannock Pass (Fig. 6, H) and just north of "Grassy Pass." A nymph, possibly belonging to this species, has also been taken at Missoula, MT. It was probably widespread in WA-ID grasslands during the Pleistocene.

54. *Auridius safra* Hamilton is a grass-feeding leafhopper endemic to the hill country of central and eastern OR and central ID. Its single site in the mountains of northeastern CA (Hamilton 1999*b*, map 1) probably represents the area of its glacial refugium.

55. *Ceratagallia gallus* Hamilton is a polyphagous leafhopper endemic to sagebrush-grassland ecotone in southeastern ID and central UT. It probably survived the glacial period and accompanying inundation of central UT on arid hillsides of the Wasatch Plateau, as has the flightless, endemic sagebrush-feeding leafhopper *Errhomus naomi* (#155).

56. *Chlorotettix similis* DeLong is a grass-feeding leafhopper of the oak savannah of BC and OR, and of Palouse grasslands from southern BC to western ID. It was probably widespread in WA grasslands during the Pleistocene.

57. *Endria montana* (DeLong & Sleesman) is a leafhopper of the Columbia basin (Wolfe 1955) and high elevation grasslands and also occurs on oak savannah in Vancouver Island, yet

it has penetrated only a short distance into Canada (Fig. 15), probably by way of the Columbia-Kootenay valley system. It apparently feeds on Letterman needlegrass, *Stipa lettermanii* Vasey, and has been taken at Rogers, MacDonald and Monida passes, from whence it has been able to invade the upper reaches of the Missouri and Yellowstone rivers. Presumably it came to the Lake Missoula valley by way of Lost Trail Pass. It has also been taken at Lolo Pass (1800 m elevation) in the Bitterroot Range and just beyond this pass on the upper reaches of the Lochsa River, a tributary of the Clearwater. Oddly, it is not known from mountains south of ID. Its glacial refugium was probably the Snake River valley of ID and MT, from whence it retreated as postglacial temperatures rose.

58. *Errhomus lineatus* (Baker) is a flightless leafhopper specialist on balsamroot, *Balsamorhiza* spp., endemic to Palouse grasslands of eastern WA, northeastern OR and western ID (Hamilton and Zack 1999, map 6). Its typical subspecies is a hybrid of 3 peripheral subspecies (see #100-102), suggesting that there were at least 3 glacial refugia. Since the parental morphs are no longer adjacent, it is impossible to tell whether this hybrid swarm originated before the latest glacial period and survived on the Palouse hills of WA, or whether it represents a highly successful postglacial hybrid that has completely swamped the intervening parental populations.

59. *Errhomus similis kahlotus* Oman is a subspecies of a widespread but flightless balsamroot-feeding leafhopper species endemic to the Columbia basin in both WA and OR. Populations of subspecies *kahlotus* Oman and its probable hybrid *dubiosus* Oman are widespread but sparse on the Columbia basin of WA. They must have survived the glacial period across most of the Columbia basin, except where intermittent Pleistocene inundations swept away populations in low-lying areas. They represent 2 of 12 subspecies of *E. similis* (see also # 106, 123-126) that reflect subdivision of the basin and eastern foothills of the Cascade Mountains of WA and OR due to canyons formed by the glacial-age rerouted Columbia River (Hamilton and Zack 1999, map 7).

60. *Hebecephalus caecus* Beamer is a grass-feeding leafhopper known only from the eastern foothills of the Cascade Range in OR (Beamer 1936) and from the mountains of southern ID just northeast of Boise. It was probably once widespread in OR-ID grasslands, but during the Pleistocene found separate refugia on the eastern slopes of the Cascades in OR and on the Snake River plains of ID.

61. *Hebecephalus callidus* (Ball) is a grass-feeding leafhopper known from the Palouse hills of WA (Ball 1899*a*), the East Kootenay valley of BC, the mountains of southern ID north of the Snake River plains, and the Bitterroot River valley of MT. It probably weathered the Pleistocene in the mountains of northern WY, and must have come to the Bitterroot valley of MT by way of Lost Trail Pass.

62. *Hebecephalus crassus* (DeLong) is a grass-feeding leafhopper known from Yellowstone Park, WY (DeLong 1926), from the Lost River Range in southeastern ID, and from Mt. Baldy (2000m elevation) in south-central BC. Its glacial-age refugium was probably in the mountains of northern WY.

63. *Hebecephalus firmus* Beamer has been taken in WA (Beamer 1936) and I have taken it near Yellowstone Park on both sides of the MT-WY border. Its glacial-age refugium was probably in the mountains of WY.

64. *Hebecephalus hilaris* Beamer is a grass-feeding leafhopper known only from the mountains of southeastern WY (Beamer 1936), and at Stevens Pass (1200m elevation) in the Cascade Range of WA on redtop *(Agrostis gigantea* Roth.), an introduced grass.

65. *Hebecephalus sagittatus* Beamer & Tuthill has been found in small numbers in scattered localities throughout the grasslands of the PNW, from the Blue Mountains of OR (Beamer and Tuthill 1935) east to the Lost River Range of eastern ID, and from the foothills of the Unita Mountains of UT north to the Okanagan Valley of BC. The Unita Mountains may

have been its glacial-age refugium. Specimens have also been taken on south-facing slopes of the Aishihik Canyon in southwestern Yukon, showing the close relationship between the grasslands of these very widely separated areas. Its spread to the Yukon may well have been accomplished before the present interglacial era (Hamilton 1997).

66. *Laevicephalus salarius* Knull is a specialist on alkali grass, *Distichlis stricta* (Torr.) Rydb. It has been found most commonly in UT on the Wasatch Plateau and in the north, but has also been taken at Kamloops in southern BC, and just north of Denver, CO. Its distribution probably reflects lack of collecting on this grass at intervening localities.

67. *Latalus curtus* Beamer & Tuthill is a grass-feeding leafhopper widespread in PNW grasslands that also has been taken at Pipestone Pass, at Lolo Pass on the MT/ID border west of Missoula, and on the upper Fraser River in central BC.

68. *Latalus mundus* Beamer & Tuthill is a grass-feeding leafhopper of PNW grasslands from the Okanagan Valley of southern BC to the Grand Teton Mountains of WY (which may have been its glacial-age refugium). It is also found in southeastern BC not far from Crowsnest Pass (probably by way of the Columbia-Kootenay valley system), at MacDonald Pass, MT, and in the Bitterroot Valley, MT, below Lost Trail Pass.

69. *Mocuellus larrimeri* (DeLong) is a grass-feeding leafhopper of PNW grasslands from scattered localities in south-central BC to western ID, and is also known from the East Kootenay of BC (probably by way of the Columbia-Kootenay valley system), Missoula, MT (DeLong 1926), and Rattlesnake Ridge in southern WA. It was probably widespread in WA-ID grasslands during the Pleistocene but has moved northwards since then. Presumably it came to MT by way of Lost Trail Pass.

70. *Norvellina rubida* (Ball) is a leafhopper that feeds on fleabane, *Eriogonum* spp. (Asteraceae), which can grow at high elevation on south-facing mountain slopes. Nevertheless, it is confined to the zone of PNW grasslands (Fig. 5, filled circles) and may have been widespread in WA-ID grasslands during the Pleistocene.

71. *Norvellina vermiculata* Lindsay is found on the Snake River plain, ID and northern UT to northwestern CO. It has also been taken just over the continental divide at White Sulphur Springs in western MT.

72. *Orocastus pinnipenis* Ross & Hamilton is a leafhopper feeding on Sandberg's blue grass, *Poa secunda* Presl. that occurs on west-facing slopes at about the 2000m level throughout most of ID and western MT (Fig. 16); elsewhere it is a valley or plateau species. It was probably widespread in ID grasslands during the Pleistocene. It has been taken in Rogers, Lemhi, Bannock and Monida passes and also close to Lost Trail and MacDonald passes, but has invaded only the fringe of the prairies, preferring the higher elevation of the Little Belt mountains of MT and the Bighorns of WY.

73. *Psammotettix attenuens* (DeLong & Davidson) is a grass-feeding leafhopper ranging from the mountains of CO to coastal BC (Fig. 17). It was probably widespread in the CO mountains and WA-ID grasslands during the Pleistocene. It has been taken in "Grassy", Lemhi and Bannock passes but has not penetrated the continental divide

74. *Sorhoanus xiphosura* Hamilton (see Part 1) is a grass-feeding leafhopper widespread through the PNW. It is tolerant of high altitudes (e.g., it is found just beyond Lolo Pass on the ID side of the border). Evidently it crosses passes readily.

### (B) DELPHACIDAE

75. *Caenodelphax atridorsum* (Beamer) was described from the eastern slopes of the Cascade Range in OR and has subsequently been discovered at two locations west of the continental divide in MT (west side of Clark Fork Valley at Missoula, and in the Blackfoot Valley).

76. *Pissonotus rubrilatus* Morgan & Beamer was described from Colorado and has

subsequently been found in widely scattered localities in WY, ID, and central BC (Bartlett and Deitz 2000).

**Taxa endemic to AB and inland BC.**

(A) CICADELLIDAE

77. *Ceratagallia okanagana* Hamilton is known only from southernmost Okanagan Valley in BC (Hamilton 1998*b*). It may have been limited to the northern part of the Columbia basin during the Pleistocene.

78. *Cuerna cuesta* Hamilton. Although not strictly confined to grasslands (Fig. 18), this forb-feeding leafhopper of BC is most often associated with grassy areas including lodgepole pine stands. Its range extends into eastern WA and northern MT. It may have been limited to the northern part of the Columbia basin during the Pleistocene. Its sister species *C. septentrionalis*, which also ranges northwards into coniferous forest glades, is entirely on other side of divide from BC to CO, crossing into the Pacific watershed only in the Yukon (Hamilton 1997).

79. *Hebecephalus planaria* Hamilton (1998*a*) is a grass-feeding leafhopper known only from southern interior of BC. It may have been limited to the northern part of the Columbia basin during the Pleistocene.

80. *Rosenus decurvatus* Hamilton & Ross is a grass-feeding leafhopper known only from south-facing bluffs above the Peace River near the BC/AB border. It probably found a glacial-age refugium on south-facing hillsides in MT and followed the retreating ice front northwards during deglaciation.

(B) DELPHACIDAE

81. *Paraliburnia furcata* Hamilton (see Part 1) is a planthopper known only from the upper Fraser River of central BC.

82. *Paraliburnia lecartus* Hamilton (see Part 1) is a planthopper known only from the Peace River district of BC. Like the preceding species (#80, 81), it probably found a glacial-age refugium on south-facing hillsides in MT.

**Taxa endemic to ID/MT border** (CICADELLIDAE only).

83. *Athysanella castor* Hamilton (see Part 1) is a leafhopper found on both sides of the ID/MT border and also across the continental divide in the Rock Creek valley of MT. It has been found just west of the divide at Lemhi Pass. It may have found a glacial-age refugium on the MT foothills to the east of the pass.

84. *Athysanella nielsoni* Blocker is a leafhopper known only from the upper Snake River valley of ID about 5 km north of Idaho Falls. A short series was taken on "sage" (Blocker and Johnson 1990), but all other species in this genus are grass feeders, and this one probably is also. It may never have moved from its glacial-age refugium, although a female that may belong to this species has been found in western ID near the junction of the Salmon and Snake rivers.

85. *Diplocolenus configuratus bicolor* Hamilton (see Part 1) has quite a restricted range although technically this leafhopper occurs in three states (Fig. 8, stars). It is confined to the continental divide and adjacent mountain ridges extending along only 400 km. During the Pleistocene it may have been restricted to the upper end of the Snake River valley. Its range now abuts that of the common eastern *D. configuratus* s.s. (#13) where they hybridize (Fig. 8, bull's-eyes).

86. *Hebecephalus crenulatus* Hamilton (1998*a*) is a grass-feeding leafhopper that has been taken from the upper Snake River plain. It may never have moved from its glacial-age refugium. Unassociated females from near the Utah border may be conspecific with this

species.

87. *Hebecephalus ferrumequinum* Hamilton (1998*a*) is a grass-feeding leafhopper that is known only from just west of Bannock Pass. It may never have moved from its glacial-age refugium.

88. *Hebecephalus picea* Hamilton (1998*a*) is a grass-feeding leafhopper that is known only from a stony plain in the Lost River valley 30 km north of the Snake River plain. It may never have moved from its glacial-age refugium.

89. *Hebecephalus pugnus* Hamilton (1998*a*) is a grass-feeding leafhopper that is known from several sites in the upper Snake River valley of ID, and near the headwaters of Lost River which flows into the Snake River plain. It probably found a glacial-age refugium on the upper Snake River valley.

90. *Hebecephalus veretillum* Hamilton (1998*a*) is a grass-feeding leafhopper that is known only from a west-facing hillside at Ketcham, ID on the north side of the Snake River plains. It may never have moved from its glacial-age refugium.

91. *Mocuellus caprillus anfractus* Hamilton (see Part 1) is a grass-feeding leafhopper with a nearly circular distribution centred around the upper Snake River valley of ID (Fig. 9, filled circles) which is probably its glacial-age refugium. It has spread to hills within 200 km N or S, and 150 km E or W. The typical subspecies (see #17) inhabits the prairies and hybridizes with this subspecies at Lemhi Pass on the ID border.

92. *Rosenus obliquus* (DeLong & Davidson) is a grass-feeding leafhopper known only from two valley sites in the mountains of south-central ID. It probably found a glacial-age refugium on the upper Snake River valley.

**Taxa endemic to Lake Missoula basin, MT** (CICADELLIDAE only).

93. *Errhomus bracatus* Hamilton & Zack is a flightless balsamroot-feeding leafhopper found only in the upper reaches of the Bitterroot valley of MT, where it seems to have found a refugium from the waters of glacial Lake Missoula (Hamilton and Zack 1999, map 9).

94. *Errhomus camensis* Hamilton & Zack is a flightless balsamroot-feeding leafhopper found only in the south of the Blackfoot valley of MT, where it seems to have found a refugium from the waters of glacial Lake Missoula (Hamilton and Zack 1999, map 10).

95. *Errhomus rivalis* Hamilton & Zack is a flightless, polyphagous leafhopper found only on the west bank of the Bitterroot River of MT, where it joins the Clark Fork River to the west of Missoula, MT. (Hamilton and Zack 1999, map 9). Since this site was under 300m of water only 12,000 years ago, it must have survived on nearby Black Mountain.

96. *Errhomus solus* Oman is a flightless, polyphagous leafhopper found on hillsides around Missoula and in the Blackfoot valley of MT (Hamilton and Zack 1999, map 9). As these sites are separated by the Clark Fork River, it must have found refugia from the waters of glacial Lake Missoula in at least two localities.

**Taxa endemic to inland OR and western ID** (CICADELLIDAE only).

97. *Ceratagallia acerata* Hamilton is known only from southernmost OR east of the Cascade Mts. (Hamilton 1998*b*).

98. *Ceratagallia clino* Hamilton is known only from the eastern slopes of the Cascade range in OR (Hamilton 1998*b*).

99. *Ceratagallia lophia* Hamilton is known only from the 1500m high summit of the Jackass Mts. in southeastern OR (Hamilton 1998*b*).

100-101. *Errhomus affinis* Oman is a flightless balsamroot-feeding leafhopper known only from the high elevations on either side of Hells Canyon on the OR-ID border (Hamilton and Zack 1999, map 9). The populations divided by this canyon on the ID side (typical subspecies, #100) and on the OR side (subspecies *attenuatus* Hamilton & Zack, #101) must predate the formation of the canyon at least 1.5 million years ago.

102. *Errhomus josephi* Oman is a flightless balsamroot-feeding leafhopper known only from high elevations in the Grande Ronde canyon of northwestern OR and adjacent WA (Hamilton and Zack 1999, map 8).

103. *Errhomus lineatus cordatus* Hamilton is now confined to the north shore of Coeur d'Alene Lake in ID, and may have survived the glacial period along the adjacent Spokane River of eastern WA where hybrids with the typical subspecies are now found.

104. *Errhomus lineatus idahoensis* Oman is now found east of the Snake River in ID and probably was confined to canyons there during the glacial maximum.

105. *Errhomus lineatus umatilla* Oman occurs in scattered localities of northeastern OR and may have been confined to the south banks of the lower Columbia canyon during the Wisconsinan.

106. *Errhomus ochoco* Oman is a flightless balsamroot-feeding leafhopper known only from the 1500m high summit of the Ochoco Mts. in central OR (Hamilton and Zack 1999, map 7).

107. *Errhomus pallidus* Oman is a flightless potentilla-feeding leafhopper known only from the foothills of the Wallowa Mts. in northwestern OR (Hamilton and Zack 1999, map 10).

108. *Errhomus serratus* Oman is a flightless balsamroot-feeding leafhopper endemic to widely separated PNW grasslands of northeastern OR and the eastern foothills of the Cascade Mountains of WA (Hamilton and Zack 1999, map 9). It must have ranged around the entire periphery of the Columbia basin before Pleistocene temperatures eliminated its northernmost populations, leaving 3 subspecies in areas which might have provided glacial refugia (see also #116, 117). The typical subspecies is found only on the southern flanks of the Blue Mts. of OR.

109. *Errhomus similis medialis* Oman, together with possible hybrids (*E. similis minutus* Oman, *E. similis nanus* Oman) and populations showing character displacement *(E. similis truncus* Oman) occurs south of the lower Columbia canyon. All may be postglacial taxa derived from a single glacial refugium.

110. *Errhomus variabilis erratus* Hamilton & Zack, is restricted to the Salmon River on the west (OR) side of the canyon.

111. *Errhomus variabilis gracilis* Hamilton & Zack is restricted to the Salmon River on the east (ID) side of the canyon.

112. *Errhomus variabilis mimicus* Hamilton & Zack is found on the southern flanks of the Blue Mts. of OR.

113. *Errhomus winquatt* Oman is a flightless balsamroot-feeding leafhopper known only from the south bank of the lower Columbia canyon where it penetrates the Cascade Mts. in southern OR (Hamilton and Zack 1999, map 8).

114. *Psammotettix greenei* Hamilton (see Part 1) is a grass-feeding leafhopper known only from southernmost OR east of the Cascade Mts. (Greene 1971).

**Taxa endemic to inland WA** (CICADELLIDAE only).

115. *Ceratagallia vipera* Hamilton is known only from the 1000m high summit of Rattlesnake Ridge, an eastern outlier of the Cascade Mts. in southern WA (Hamilton 1998*b*).

116-117. *Errhomus brevis* Oman is a flightless balsamroot-feeding leafhopper known only from the north bank of the lower Columbia canyon and inland regions of southern WA adjacent to the Cascade Mts. (Hamilton and Zack 1999, map 6). The canyon populations (typical subspecies, #116) and inland ones (subspecies *simcoe* Oman, #117) form hybrid swarms where they meet at the mouth of the Klickitat River (idem, map 11).

118. *Errhomus calvus* Oman is a flightless polyphagous leafhopper known only from the

Okanogan highlands of northern WA and adjacent BC (Hamilton and Zack 1999, map 2).

119. *Errhomus paradoxus* Oman is a flightless balsamroot-feeding leafhopper known only from the northern bank of the lower Columbia canyon in southern WA just to the east of the range of *Errhomus brevis* (Hamilton and Zack 1999, map 8).

120. *Errhomus picturatus* Hamilton & Zack is a flightless balsamroot-feeding leafhopper known only from a single site near Wenatchee Lake in northwestern WA adjacent to the Cascade Mts. just to the east of the range of *Errhomus wolfei* (Hamilton and Zack 1999, map 8).

121. *Errhomus praedictus* Hamilton & Zack is a flightless balsamroot-feeding leafhopper known only from a single site on the south slopes of the Simcoe Mts. in southern WA just to the east of the range of *Errhomus brevis* (Hamilton and Zack 1999, map 8, as *inconspicuus* [sic]).

122. *Errhomus reflexus* Oman is a flightless balsamroot-feeding leafhopper known only from two populations on either side of the Kittitas Valley in central WA east of the Cascade Mts. (Hamilton and Zack 1999, map 8).

123. *Errhomus satus* Oman is a flightless balsamroot-feeding leafhopper known only from just north of Satus Pass in the Simcoe Mts. in southern WA just to the east of the range of *Errhomus brevis* (Hamilton and Zack 1999, map 8).

124. *Errhomus serratus instabilis* Oman is found only in the Naches valley of WA.

125. *Errhomus serratus obliteratus* Hamilton occurs on the arid eastern slopes of the Wenatchee Mts. of WA.

126. *Errhomus similis* Oman, typical subspecies, and its probable hybrids *E. similis confinis* Oman and *Errhomus similis relativus* Oman, occur on the eastern foothills of the Cascade Mountains on WA.

127. *Errhomus similis sobrinus* Oman is confined to the angular bend made by the Columbia in the Pascoe Basin, WA. This appears to be an area that was east of the Columbia until the river shifted to its present location at least 5 million years ago.

128. *E. similis socius* Oman is confined to an area to the west of the Columbia canyon in WA south of Lake Chelan and north of the Wenatchee River canyon.

129. *Errhomus similis zonarius* Oman is found north of the Columbia canyon and east of the Okanagan valley in WA.

130. *Errhomus variabilis* Oman is a flightless balsamroot-feeding leafhopper endemic to the northern edge of the Columbia basin of WA, and the Snake River valley on the ID-OR boundary (Hamilton and Zack 1999, map 10). Its various subspecies reflect at least 4 glacial-age refugia, the typical subspecies being found on the Columbia basin and the others (#107-109) in peripheral areas.

131. *Errhomus wolfei* Oman is a flightless balsamroot-feeding leafhopper known only from the Wenatchee River canyon of northwestern WA (Hamilton and Zack 1999, map 8).

132. *Limotettix zacki* Hamilton is known only from the 300m high summit of Badger Mt. just west of the Columbia River in WA (Hamilton 1994*a*).

**Taxa endemic to Pacific coast north of CA** (CICADELLIDAE only).

133. *Athysanella valla* Blocker and Johnson is a grass-feeding leafhopper known only from southernmost OR west of the Cascade Mts. (Blocker and Johnson 1990).

134. *Ceratagallia omani* Hamilton is known from Saturna I. off Vancouver Island, BC, along the entire OR coast, and inland on the Coast Range as high as 1000m (Hamilton 1998*b*).

135. *Evacanthus lacunar* Hamilton is a *Scrophularia*-feeding leafhopper known only from Marys Peak (1100m) in the Coast Range of OR (Hamilton 1983).

136. *Latalus occidentalis* (DeLong) is known from Marys Peak and adjacent coast of OR, and possibly also from Vancouver Island in BC (based on an unassociated female). This

species appears to be a closely related to an undescribed species from 1100m elevation in the Cuyamaca Mts. of southernmost CA.

137. *Limotettix beameri* (Medler) is found along the coast of OR including the Coast Range, and near Puget Sound in WA.

138. *Psammotettix diademata* Hamilton (see Part 1) is known only from the shore of the Queen Charlotte Islands in BC (Fig. 2, star).

139. *Psammotettix nesiotus* Hamilton (see Part 1) is known only from both sides of the Strait of Georgia that separates Vancouver Island from mainland BC.

**Taxa endemic to mountains of CO and adjacent WY.**

(A) CICADELLIDAE

140. *Athysanella gardenia* Osborn was described from the mountains of CO and has subsequently been recorded from both CO and WY (Blocker and Johnson 1988) without any more specific information. Its circumscribed distribution seems to indicate montane endemism.

141. *Athysanella hyperoche* Hamilton (see Part 1) is known only from a pass in the Laramie Mountains of WY (see Part 1).

142. *Diplocolenus configuratus nigrior* Ross & Hamilton is a rather rare grass-feeding leafhopper known only from mountains in AZ and CO (where it probably found glacial-age refugia), and across about 200 km of the foothills of the Unita Mts. on the borders of ID, UT and WY (Fig. 8, filled circles) to the west of *D. configuratus*. It appears to hybridize (Fig. 8, bull's-eyes) with both *D. configuratus* s.s. and *D. configuratus bicolor*.

143. *Errhomus montanus* (Baker) is a flightless potentilla-feeding leafhopper found on high mountains from CO and western WY to southern MT (Hamilton and Zack 1999, map 1). It was probably more widely distributed during the Pleistocene, and has since retreated into its montane fastness as temperatures increased 10,000 years ago.

144. *Hebecephalus chandleri* Hamilton is a grass-feeding leafhopper known only from the Bighorn Mountains of northern WY (Hamilton 1998*a*). It is a sister-species of *H. atralbis* Emeljanov from Siberia.

145. *Hebecephalus vinculatus* Ball is a grass-feeding leafhopper found in the mountains of CO (Ball 1899*b*). It was incorrectly recorded from WY and Labrador (see Hamilton 1998*a*)

146. *Idiodonus josea* (Ball) is a leafhopper of the mountains of CO and southern MT (near Yellowstone N.Pk.) Nymphs that are also reddish, but evenly coloured instead of maculate, perhaps may be conspecific; these are known from southern BC and adjacent ID.

147. *Norvellina saucia* (Ball) is known only from the mountains of CO (Lindsay 1940).

148. *Orocastus hyalinus* (Beamer) is a grass-feeding leafhopper known only from the mountains of CO (Beamer 1938).

149. *Psammotettix viridinervis* Ross & Hamilton is a grass-feeding leafhopper known only from the mountains of southeastern WY (Ross and Hamilton 1972).

150. *Sorhoanus involutus* Hamilton (see Part 1) is known only from the mountains of CO.

(B) DELPHACIDAE

151. *Kosswigianella irrutilo* Hamilton (see Part 1) is known only from the mountains of CO. It has no known relatives.

**Taxa endemic to northern UT and adjacent WY**

(A) CICADELLIDAE

152. *Athysanella obscura* Johnson is known from "Antelope, UT" (Johnson and Blocker 1979) and an unspecified locality in WY (Blocker and Johnson 1990).

153. *Hebecephalus abies* is a grass-feeding leafhopper that is only known from the foothills of the Unita Mountains and the West Tavaputs Plateau of UT (Hamilton 1998*a*).

154. *Hebecephalus filamentus* Hamilton & Ross is a grass-feeding leafhopper that occurs in northeastern UT and also on the mountains of southeastern WY (Hamilton 1998*a*).

155. *Mocuellus quinquespinus* Hamilton (see Part 1) is a grass-feeding leafhopper that is only known from a single locality in the foothills of the Unita Mountains of UT (Fig. 9, star), an area particularly rich in PNW grassland leafhoppers, including *Hebecephalus abies* (# 149).

156. *Norvellina curvata* Lindsay is known only from the Grand Teton Mountains of WY (Lindsay 1940).

(B) DELPHACIDAE

157. *Achorotile apicata* Hamilton (see Part 1) is a planthopper known only from the Unita Mountains of northeastern UT. It is related to a transboreal species.

158. *Elachodelphax unita* Hamilton (see Part 1) is a planthopper known only from the Unita Mountains of northeastern UT. It is related to *E. mazama* (#40) from the Cascade Mountains of WA.

### Taxa endemic to mountains of central UT

(A) CICADELLIDAE

159. *Errhomus naomi* Hamilton & Zack is known only from an isolated location in the Fish Lake mountains of the Wasatch Plateau, UT. Its relatives inhabit western MT. It feeds on the common species of the Great Plains, hoary sagebrush (*Artemisia cana* Pursh) rather than on the common Rocky Mountain species (*A. tridentata* Nutt.)

(B) DELPHACIDAE

160. *Kosswigianella wasatchi* Hamilton (see Part 1) is a planthopper known only from the Wasatch Plateau of central UT. It is related to a transcontinental species.

## CONCLUSIONS

**Endemism.** Endemics account for approximately half (44%) of the entire PNW grassland fauna of 275 taxa. If one adds the 22 taxa that are endemic to the mountains of CO, UT and WY the total endemic fauna rises to 142 taxa (52% of the PNW fauna). This is one of the highest percentages of regional endemism in North America. The total number of endemics is third only to those of the prairies and desert grasslands. Clearly this represents an unique fauna of great age that has managed to survive Pleistocene climate change in some refugium. But where? This can be determined only after deducing how much the fauna moved in response to postglacial (Hypsithermal) warming, and to what degree mountain passes proved to be a barrier to dispersal.

**Hypsithermal change**. The only valleys in the PNW with few endemics and limited southern faunal elements are the isolated glaciated valleys of central and eastern BC. These valleys must have been repopulated largely by prairie insects coming over "Crooked River" and Crowsnest passes, for they are essentially an Alberta fauna found mainly along the upper Fraser River (#1, 8, 14, 21, 27, 31) and in the East Kootenay valley (#1, 2, 9, 19, 24, 26, 28). This faunal invasion probably occurred during the Hypsithermal as these passes are now completely forested for many kilometres. Hypsithermal grasslands probably extended as far north as the Mackenzie River but not into the Yukon (Hamilton 1997; see also #50). Faunal exchange this far north was probably at a still warmer time, possibly during the height of the Sangamon interglacial 124,000 years ago (Matthews 1979).

It is unlikely that Hypsithermal warming ever brought together ranges of PNW grasslands sufficiently to permit free faunal interchange. Widely dispersing leafhoppers seldom are found throughout PNW grasslands. For example, the endemic leafhoppers *Norvellina rubida* (#70) and *Sorhoanus xiphosura* (#74) range throughout much of the PNW grasslands from Wyoming to southern British Columbia, but, even more than the grasslands themselves, they have fragmented ranges (Fig. 5, filled circles and stars).

**PNW-prairie passes**. In the U.S.A. there is a sharp division between faunas of the PNW grasslands and those of the prairies. As the two are connected across a number of grassy passes (Fig. 6) and are botanically identical on both sides, this becomes hard to understand with our present knowledge. Yet there are at least 59 prairie taxa that range up to the continental divide; at least six do not cross it at all (the typical subspecies of #32-35, plus *Stenometopiellus cookei*, sister-species of #38, and *Elachodelphax borealis*, sister-species of # 40), while 31 penetrate only a short way into the PNW (#1-31). Five taxa that inhabit the PNW do not cross these passes although they range up to them (#53, 67, 68, 73, 91). Four PNW endemics have crossed the divide to invade adjacent foothills prairie (#51, 62, 72, 83). Another 18 PNW taxa which range up to the continental divide appear to be confined to mountains or high latitudes (#62-64, 74, 76, 85, 87, 140-151) and are therefore unlikely to invade the prairies.

Yet despite the few cases of faunal exchange between these grasslands, there are many passes in MT, ID and WY which show numerous cases of insect migrations (Table 1). Three components seem to govern whether passes are suitable for leafhopper dispersal.

Predictably, "open" (grassland) passes have the largest number of grassland leafhopper taxa. The wide pass at Great Divide Basin, WY was probably a conduit for 14 species, but only a single grassland species has been taken actually in the pass which is now very arid. A similar number probably crossed Bannock Pass, and 10 are still found there. Less certain evidence has been found that "Grassy Pass" also has been the conduit for 14 species, of which only three have been found in the pass. Ten to 12 taxa can be inferred to have crossed through Lemhi, Monida and Lost Trail passes. Possibly "Grassy," Lemi and Monida Trail passes have been open grasslands only recently, having been forested during the Pleistocene, and then arid during the Hypsithermal. Lost Trail Pass is currently forested on its southern flank, but might have been open during the Hypsithermal.

Elevation is the second most important component governing whether leafhoppers can use passes. Crowsnest Pass in southern BC (1400 m) and Rogers Pass, one of the lowest passes in MT (1800 m), are both good leafhopper conduits (for 11 taxa each). MacDonald Pass (2000 m) has a substantially smaller number of taxa associated with it (eight taxa, four in the pass). Increasing elevation of passes south of this is offset by the increasing elevation of the montane grassland at this latitude, so that Lemhi and Bannock on the ID/MT border (both at 2200 m) are "open" passes through which at least 12 taxa have passed.

Direction of the pass also seems to play an important role in dispersal of leafhoppers. The passes most used by leafhoppers tend to have a north-south extent. East-west passes such as MacDonald Pass (2000 m) and Chief Joseph, MT (2200 m) show much less influence in leafhopper spread than one would expect. The direction of transfer has been mainly north to south at "Crooked River," Rogers and Monida passes, and south to north at "Grassy Pass". In each case the dominant direction is from the prairies into the intermontane grasslands, and not *vice versa*. Probably the winds that aid most in leafhopper dispersal are the strong prairie southerlies of summer. The prevailing northwesterlies of spring and fall appear to occur too early and late to transfer gravid females. Such winds would carry Homoptera over local barriers formed by north and east-facing slopes, which are cooler and not as suitable for grassland insects.

**Refugia**. There are 32 widespread PNW grassland Homoptera (#34, 36, 41-43, 51, 52-76) that may be either widely dispersing or merely disjunct relicts of a formerly widespread distribution. These include 20 taxa (#34, 36, 41-43, 51, 53, 54, 63, 65-76) which fail to match each other in distribution (e.g., Fig. 5) so no conclusions can be reached about their Pleistocene distribution. The probability is greatest that these have each survived the Pleistocene in more than one refugium, from whence they have spread to outlying areas in a discordant manner. Three other such species are *Endria montana* (#57) whose range is divided between grasslands on southern Vancouver Island, BC and those of the Rocky Mountains, centred around the upper end of the Snake River Valley; *Hebecephalus caecus* (#60) whose range is divided even today between the eastern slopes of the Cascades in OR and upper end of the Snake River Valley; and *Hebecephalus hilaris* (#64) which is known only from the Cascade Range of WA and the mountains of southeastern WY.

By contrast, there are 80 taxa endemic to just a part of the PNW (#45-52, 77-151). The most strikingly different PNW grassland fauna is that of oak savannah and other Coast Range grasslands such as the grassy "bald" above 1200 m elevation on Marys Peak, OR (Fig. 5, filled triangle), the latter with two endemic species (#135, 136). This coastal grassland shares with inland sites only three PNW leafhoppers (#56, 57, 73; see Figs. 15, 17). Seven grassland taxa (#133-139) are restricted to the Pacific coast side of the Cascade range. One of these, *Psammotettix diademata* (#138) is known only from the shores of the Queen Charlotte Islands far to the north of other PNW grasslands. These islands also have one other endemic leafhopper, *Evacanthus grandipes* Hamilton (1983) and an endemic spittlebug, *Aphrophora regina* Hamilton (1982), both of which are forest insects, so the weather on the seaward side of the islands was probably mild enough for all three of them to weather Pleistocene glaciation there. Further evidence that the Queen Charlotte Islands were not glaciated during the last ice advance is provided by Nearctic earthworms, that exist here and on Vancouver Island although eradicated from the rest of Canada by glaciation (Hendrix and Bohlen 2001, fig. 1).

Other geographic areas with distinctive faunas, from north to south, are inland BC plus AB with six taxa (#77-82), eastern ID plus adjacent MT with 10 taxa (#83-92), inland WA with 18 taxa (#115-132), and inland OR plus western ID with 18 taxa (#97-114). Do these four geographic areas represent four additional Pleistocene refuges? Concurrence between individual distribution patterns should resolve this question.

In addition to these 54 localized taxa endemic to inland PNW grasslands, there are six leafhoppers that represent three pairs of sister taxa with widely disjunct ranges (#45-52). Three of these, one from each pair, are associated either with the eastern slopes of the Cascade Mountains in OR (#45, 48), or with the Cascades themselves in the south of OR (#52). Their sister-taxa are found either on the upper reaches of the Clark Fork river in MT (#46, 47) or are widely dispersed around the drainage basin of the Columbia River and the Clark Fork river (#51). This suggests a PNW-wide dispersal pattern that became fragmented into an OR component associated with the southern Cascades, a Columbia basin component, and a Clark Fork component; subsequent catastrophic flooding of the Columbia basin in the late Pleistocene may have wiped out intervening populations of all but the species most adapted to high elevations, *Sorhoanus debilis* (#51). This disjunct distribution pattern is similar to that of *Hebecephalus caecus* (#60), discussed above. Confirmation of a fragmented grassland habitat is found in the several groups of local endemics that mirror this pattern, as well as some widespread prairie species whose PNW range is separated by hundreds of kilometres, e.g., *Flexamia inflata* (Osborn & Ball) (Whitcomb and Hicks 1988, Fig. 41).

The easternmost of these disjunct grasslands occurs along the upper reaches of the Clark Fork River from St. Regis, MT to the continental divide. This area has seven of the eight endemic leafhoppers of MT (#46, 47, 93-96, plus *Macrosteles skalkahiensis* Beirne from 2200 m elevation in Skalkaho Pass, east of the Bitterroot Valley: Beirne 1952). Most of these endemics are members of the flightless genus *Errhomus*. Three (#93, 94, 96) inhabit two of the four main tributaries of the valley that was once Lake Missoula: the Bitterroot and

Blackfoot rivers. A fourth (#95) is found on the west bank of the Clark Fork river where these rivers converge at Missoula. This flightless species must have survived inundation of the valley on south-facing mountain slopes at least 300 m higher that its present locality. Another genus is represented along the third tributary, Rock Creek: *Athysanella repulsa* (#46).

A much larger number of local endemic taxa are associated with the land to the east of the Cascade Range in WA and OR (#45, 48, 52, 60, 97, 98, 106, 109, 113, 114, 116-129, 131, 132), a total of 27 endemics in this area. Sixteen of these species are highly localized, flightless leafhoppers of WA and adjacent OR (#107, 108, 116-129, 131), and two of these each have two subspecies (#116, 117; 124, 125) in adjacent areas, suggesting occupancy of this area for a considerable time. Three others appear to have had another refugium in southwestern OR (#52, 97, 114). Two became stranded on isolated mountain crests east of the Cascades in WA (#115, 132). Two species are known from single hills in south-central OR (#99, 106). It appears clear that at least patches of grassland survived along with their leafhopper faunas in numerous isolated situations, probably south-facing hillsides and canyon slopes. The only species of *Errhomus* that inhabits the most arid parts of the Columbia plateau, *E. similis*, now favours north and east-facing slopes of coulees that are not so subject to drought as level ground or south and west-facing slopes (Hamilton and Zack, 1999). This suggests that they found glacial-age refugia on south-facing slopes. The grasslands of WA were probably more severely modified than those of OR, resulting in a much more fragmented WA fauna.

The intervening area between these eastern and western grasslands is largely Columbia basin. There, 13 endemic taxa are members of the flightless leafhopper genus *Errhomus* which feed on arid-adapted perennial composites: four in WA and adjacent ID (#58, 59, 103, 130) and nine along Hell's Canyon on the ID/OR border, and up into the Blue Mountains of OR (#100-102, 104, 105, 107, 108, 110-112). All other, more mobile endemic leafhoppers have migrated northwards from the Columbia basin, usually into many adjacent areas (#32, 33, 35, 56, 78 and probably many of the widely dispersing species). Four (#39, 40, 77, 79) are known only from glaciated valleys in southern BC and northern WA and must have come from refugia further south.

Nine species belonging to five genera (#38, 61, 84, 86, 88-92) are associated with the headwaters of the Snake River and one (#60) has a disjunct population associated with a tributary river northeast of Boise in the western part of the state. Curiously, none are members of *Errhomus* although the genus is speciose both east and west of this valley. Pleistocene volcanism that flooded much of the Snake River valley in ID may have decimated populations of this arid-adapted genus. Other leafhoppers may have survived in this region through their greater powers of dispersal. For example, *Mocuellus caprillus anfractus* (#91) has a nearly circular range strongly suggestive of dispersal from a single valley bottom refuge. The other species are scattered in various valleys along the south-facing slopes of the ranges crossing central ID or the upper Snake canyon where it penetrates the WY border. This pattern is highly suggestive of a Pleistocene rain-shadow grassland in the upper Snake River plains, together with isolated grassland patches on south-facing slopes from the Lost River Range westward to the present site of Boise.

Other leafhoppers may have adapted to cooler conditions during the Pleistocene, and subsequently sought refuge after glaciers melted by migrating to higher elevation grasslands. Some PNW endemics (e.g., #55) are now limited to a few valley bottom sites in a linear pattern suggesting migration north from a glacial refugium. At least four widespread species (#20, 27, 43, 73) have migrated far northwards into glaciated areas. Four others (#29, 51, 62, 72) are now found in mountains or grasslands at lower elevation less far north. One (#37) is known only from a glaciated mountain. Fifteen other endemic taxa are characteristic of limited areas of the Rockies of southern MT/ID (Bitterroot Range) south to CO (#83, 85, 87, 140-151). These may have shifted their ranges vertically rather than longitudinally, in the same manner that nine endemics in UT and adjacent WY (#152-160) almost certainly have done. One flightless species (#143) and two others (#142, 146) are presently found in isolated mountains in three states, so the refugium may have extended a considerable distance along the mountain range. One species (#144) is presently confined to the Bighorn Mountains of north-central WY, which may represent an isolated grassland refugium.

Three species are presently known only from the "Crooked River" Pass vicinity, on the upper Fraser River of BC (#81) and south-facing bluffs along the Peace River in Alberta (#80, 82). These may once have been inhabitants of the eastern slopes of the Rockies; but this would require a very extensive displacement northwards during the Hypsithermal not evident among other Homoptera.

**Pleistocene climate.** There is ample evidence that PNW grasslands and their fauna are endemic phenomena. Indeed, there is only evidence for a Hypsithermal invasion of prairie grasslands into two northern, deglaciated mountain valleys. How, then, can one reconcile the biological evidence for extensive endemism with the geological evidence for extensive permafrost patterns across the breadth of the PNW?

First, glacial-age circular features known as "stone rings" may not be indicative of permafrost at all. That they have been cited as evidence of permafrost (Brunnschweiler 1962) may be due to superficial similarities to ice mounds in modern tundra. This view has not found favour among modern geologists (Matthews 1979). Stone rings are found only on tablelands in the PNW (Fig. 19). These structures may point towards yearly alternations of extremes of heat and cold. They were probably formed of rock fragments forced outwards around the edges of ponds that froze solid each winter, then completely melted again each summer, leaving a depression to collect yet more water and thus grow to a larger size each successive year.

Second, land slope and direction are obvious components of microclimate. South-facing slopes are particularly subject to aridity and high summer temperatures; west-facing slopes show similar but less severe conditions and are the modern preferred habitat of PNW grassland leafhoppers. A number of endemic grassland leafhoppers in the Yukon are associated with south-facing slopes (Hamilton 1997). That such a phenomenon was very much a part of glacial-age ecology is shown by pollen and subfossil assemblies in the Saint Lawrence valley of Québec (Mott et al. 1981). At a time when the whole valley was extensive "spruce-aspen forest" following the retreat of "tundra" conditions 10,000 years ago, Mont St. Hilaire had high levels of oak pollen and even an oak-feeding treehopper (Membracidae), presumably from the sun-warmed slopes.

Thirdly, timing is probably a factor. Permafrost soil structures indicate the overall coldness of a site, but not the duration of that cold. Thus, a long and severe winter could well be succeeded by a mild (perhaps even hot) but short summer. This is probably the explanation of why the majority of endemic flightless leafhoppers in *Errhomus* have survived the Pleistocene on the Columbia Basin by feeding on a spring-flowering host, balsamroot.

In total, 38 PNW-endemic taxa belong to *Errhomus* (#58, 59, 93-96, 98-105, 109-114, 116-131, plus six subspecies of postglacial origin). These often occupy adjacent territories that follow geological features erased long before the Pleistocene (Hamilton and Zack 1999). The evidence is thus strong that these regions suffered little climate change during the Pleistocene, although the extent of the arid areas of the Columbia basin were probably more limited than at present. *Errhomus* are mostly insects that emerge early in spring to take advantage of perennials that dry up in summer. During the Pleistocene their hosts may have grown in mid-summer instead of springtime. If these leafhoppers are active during cool weather, they would have been able to adjust their seasonality so that their ranges were little affected by Pleistocene conditions.

Nine of the 12 balsamroot-feeding species of *Errhomus* in WA and OR are found very close to (but not on) ring-patterned ground (Fig. 19, # 1-9). Six exceptions to this lifestyle are only found in the most northerly or montane species: *E. calvus* (Fig. 19, # 10) north of the Columbia, *E. pallidus* in the Blue Mountains of OR (Fig. 19, # 12), *E. solus* and *E. rivalis* (Fig. 19, # 14-15) near the deepest part of the Lake Missoula valley, *E. montanus* in the highest mountains of CO and WY, and *E. naomi* above 3000 m in the Wasatch Plateau of UT. All have shifted to other hosts, probably when balsamroot became scarce under Pleistocene conditions. In all of the glaciated area east of OR, only the highly localized *E. camensis* (#94) still feeds on balsamroot.

Additional evidence for short but warm Pleistocene summers close to ice margins comes from eastern Canada. There, the endemic Gulf of St. Lawrence aster, *Aster lautentianus* Fernald is presumed to have weathered the Pleistocene on the ice-free Magdalen Is and subsequently spread to adjacent deglaciated coasts of New Brunswick and Prince Edward I (Hamilton 2002, fig. 2). This aster flowers after two to three months, as contrasted to its continental relatives *A. brachyactis* Blake and *A. frondosus* (Nutt.) T. & G. at six to eight months each (Houle and Haber 1990).

How hot was the PNW glacial age summer? East of the Rockies and south of the ice sheet, summer was much cooler than at present except in the far south (Brunnschweiler 1962). This was probably due to extensive cloud cover associated with increased precipitation. Prairie-like conditions ("periglacial grassland") existed only close to the ice front (Hamilton 1994*b*) where a permanent high pressure system over the glacier field suppressed summer rainfall. South of the PNW there is also evidence of reduced evaporation and increased precipitation: glacial-age Lake Bonneville completely filled the northwestern valley of UT to overflowing (it is now shrunk to Salt Lake). But, as in eastern North America, summer temperatures near the ice front may well have been close to spring temperatures today. Evidence for this in western North America comes from four endemic species (#80-82, 138) associated with the northern grasslands of the Peace River in AB, the upper Fraser River and on the Queen Charlotte Islands of BC. Such a suppression of rainfall is indicated by the distribution of loess in the PNW, which would have been driven from glacial moraines southward with strong winds off the ice sheet across treeless areas, and deposited where open vegetation (grasslands or open woodlands) broke the force of the wind. Major loess deposits on the Columbia basin as far south as the Blue Mountains of OR, and on the Snake River plains of ID, suggest the presence of open forests or grasslands there (Fig. 20).

Conversely, the numerous glacial-age lakes across UT, NV and southern OR show that these areas were cooler and wetter than at present. This belt must have been a zone of constant frontal activity between a stationary high-pressure system over the ice sheet, and a stationary low-pressure system over the semideserts of Arizona and New Mexico (Fig. 20). Between these two pressure systems the prevailing winds would have been driven from east to west, drawing moisture from the Gulf of Mexico northwestward towards UT. This would have constituted a real monsoon system, reversing the usual air flow patterns of the winter season.

**Summary.** At least nine PNW Pleistocene grasslands can be deduced. These are listed in descending importance as refuges for leafhoppers and planthoppers:

(1) east slopes of the Cascade Range (Fig. 2C), from Washington state to northern California, with 27 endemics, two of which are sister species of Montana endemics;
(2) Columbia basin (Fig. 2E) including Palouse hills of Washington and canyons of western Idaho, with 22 endemics, mostly with flightless females incapable of traversing deep canyons;
(3) Rocky Mountains of Montana south to Colorado (Fig. 2J) where 19 endemics must have persisted on grassy south-facing slopes close to their present highly restricted ranges;
(4) the Snake River and south-facing slopes north of the Snake River in southern Idaho (Fig.

2F) must have been grassland near the headwaters, as all 12 endemics are found in that end of the valley;

(5) the Pacific coast, Mary's Peak (Fig. 5, triangle) and the Willamette Valley (Fig. 2B) west of the Cascade Range of Oregon have nine endemics;

(6) the Upper Clark Fork valley in western Montana (Fig. 2G) has six grassland endemics (including ones with flightless females) which must have survived the Pleistocene on the edges of glacial Lake Missoula;

(7) grassland patches along the upper Fraser and Peace rivers of BC have three endemics which are deep in glaciated areas and must have come from grasslands east of the Continental Divide (Fig. 2H, northern end); these and possibly a single widespread PNW species (#50) with a similar distribution along the Fraser and Peace rivers to the Mackenzie River are probably remnants of a periglacial grassland near the ice front in Alberta;

(8) the mountains of south-central OR (Fig. 2D) have two endemics; and

(9) the coast of the Queen Charlotte Islands (Fig. 2, star) has a single endemic grassland leafhopper. Other grasslands on islands further south (Fig. 2A) were repopulated by hypsithermal invasion.

Additional refugia might have been in the mountains of Utah and adjacent Wyoming, but these may have been further southwards.

## ACKNOWLEDGEMENTS

This study is the outcome of 23 years of leafhopper surveys (1948-1971) by H.H. Ross to document the leafhopper fauna of North American grasslands, and is dedicated to the memory of "Herb." He and his students took more than 1,400 samples, beginning on July 16, 1948 at Ozark, Illinois (note code GL 109). This work was continued by R.F. Whitcomb and myself. The Pacific Northwest maps were based on an original prepared by Bonnie Hall for Oregon State University, used by permission. The manuscript was reviewed by D. Lafontaine of AAFC, Ottawa.

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## FAUNAL SYNOPSIS AND INDEX

to species numbered in text
(*) indicates taxa of probable post-glacial origin

| | |
|---|---|
| *A. cosmeticus* Hamilton | #47 (MT) |
| *A. helvus* (DeLong) | #7 (prairie) |
| *A. ordinatus* (Ball) | #8 (prairie) |
| *A. o. crocatus* Hamilton | #34 (PNW) |
| *A. safra* Hamilton | #54 (PNW) |
| *A. vitellinus* Hamilton | #48 (OR) |
| *Balclutha confluens* (Rey) | **northern** |
| *B. manitou* (Gillette & Baker) | **northern** |
| *B. neglecta* DeLong & Dav.) | prairie |
| *B. punctata* (Fabricius) | **northern** |
| *Ballana* spp. (11) | southern |
| *B. atridorsum* (Van Duzee) | prairie |
| *B. chrysothamna* DeLong | ? (ID) |
| *B. curvidens* DeLong | ? (ID) |
| *B. ortha* DeLong | prairie |
| *B. spinosa* DeLong | ? (ID-OR) |
| *Carsonus aridus* (Ball) | southern |
| *C. furcatus* (Oman) | southern |
| *C. irroratus* (Ball) | southern |
| *Ceratagallia acerata* Ham. | #97 (OR) |
| *C. arida* (Oman) | #9 (prairie) |
| *C. artemisia* Oman | southern |
| *C. californica* (Baker) | southern |
| *C. clino* Hamilton | #98 (OR) |
| *C. gallus* Hamilton | #55 (ID-UT) |
| *C. lophia* Hamilton | #99 (OR) |
| *C. nanella zacki* Hamilton | #35 (BC-WA) |
| *C. okanagana* Hamilton | #77 (BC) |
| *C. robusta poudris* (Oman) | southern |
| *C. omani* Hamilton | #134 BC/OR) |
| *C. siccifolia* (Uhler) | **northern** |
| *C. siccifolia compressa* H. | #36 (PNW) |
| *C. vipera* Hamilton | #115 (WA) |
| *C. viator* Hamilton | #10 (prairie) |
| *C. vulgaris* (Oman) | #11 (prairie) |
| *Chlorotettix similis* DeLong | #56 (BC/ID/ OR) |
| *Colladonus aureolus* (Van D.) | southern |
| *Commellus sexvittatus* (V. D.) | prairie |
| *Cuerna cuesta* Hamilton | #78 (BC-MT-WA) |
| *Deltocephalus artemisiae* Gillette & Baker | prairie |
| *D. fuscinervosus* Van Duzee | southern |
| *D. minutus* Van Duzee | southern |
| *D. vanduzeei* Gillette & Baker | ? (PNW) |
| *D. vanfus* Kramer | southern |
| *Diplocolenus brevior* R. & H. | **northern** |
| *D. configuratus* (Uhler) | #13 (prairie) |
| *D. c. bicolor* Hamilton | #85 (ID-MT-WY) |
| *D. c. nigrior* Ross & Hamilton | #142 (AZ-ID) |
| *D. evansi* (Ashmead) | **northern** |
| *Draeculacephala bivoltina* H. | southern |
| *D. borealis orea* Hamilton | ? (PNW) |
| *D. crassicornis* Van Duzee | ? (PNW) |

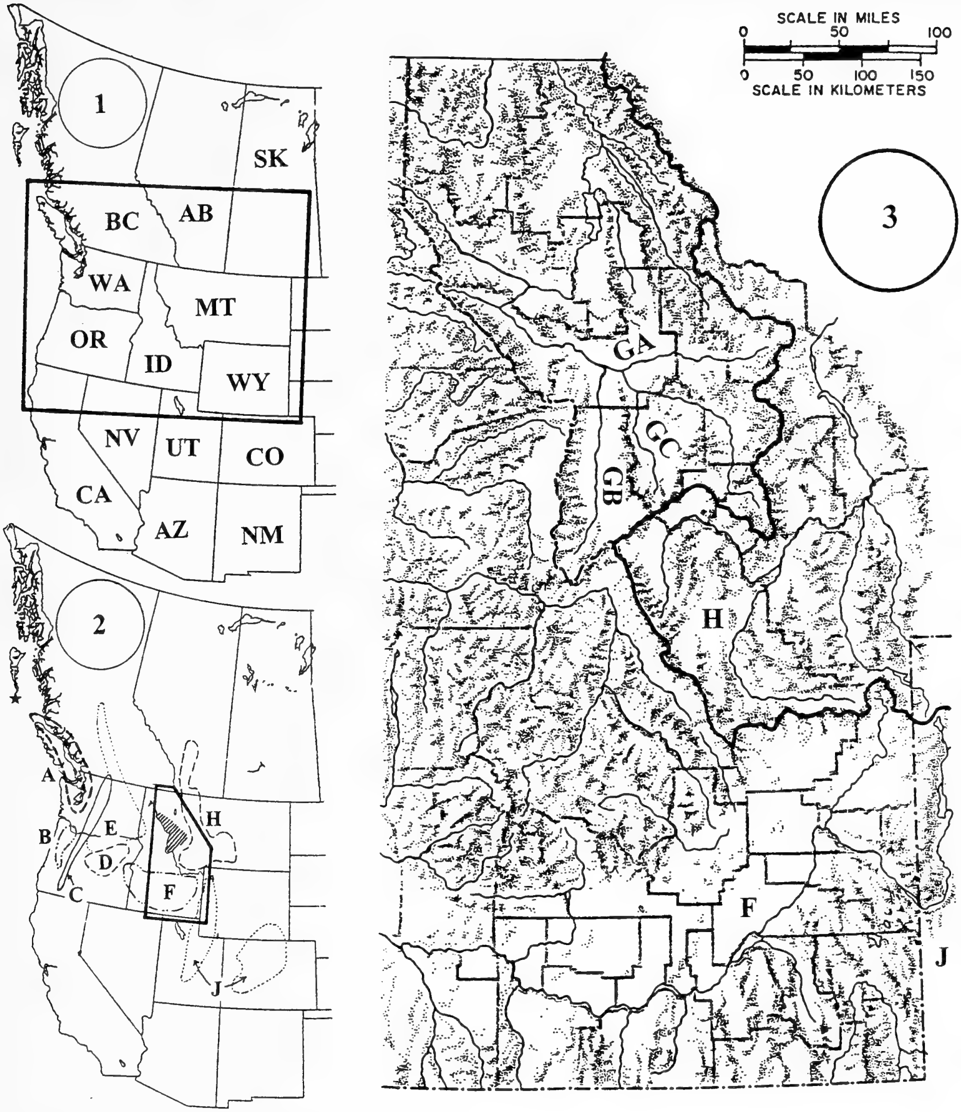
| | |
|---|---|
| *D. robinsoni* Hamilton | **northern** |
| *Elymana circius* Hamilton | #14 (prairie) |
| *Endria inimica* (Say) | prairie |
| *E. montana* (DeLong & Sl.) | #57 (PNW) |
| *Errhomus affinis* Oman | #100 (ID) |
| *E. affinis attenuatus* Hamilton | #101 (OR) |
| *E. bracatus* Hamilton | #93 (MT) |
| *E. brevis* Oman | #116 (WA) |
| *E. brevis simcoe* Oman | #117 (WA) |
| *E. calvus* Oman | #118 (BC-WA) |
| *E. camensis* Hamilton | #94 (MT) |
| *E. josephi* Oman | #102 (OR-WA) |
| *E. lineatus* (Baker) | #58 (WA) |
| *E. lineatus cordatus* Hamilton | #103 (ID) |
| *E. lineatus idahoensis* Oman | #104 (ID) |
| *E. lineatus umatilla* Oman | #105 (OR) |
| *E. montanus* (Baker) | #143 (CO/ MT-WY) |
| *E. naomi* Hamilton | #159 (UT) |
| *E. ochoco* Oman | #106 (OR) |
| *E. pallidus* Oman | #107 (OR) |
| *E. paradoxus* Oman | #119 (WA) |
| *E. picturatus* Hamilton | #120 (WA) |
| *E. praedictus* Hamilton | #121 (WA) |
| *E. reflexus* Oman | #122 (WA) |
| *E. rivalis* Hamilton | #95 (MT) |
| *E. satus* Oman | #123 (WA) |
| *E. serratus* Oman | #108 (OR) |
| *E. s. instabilis* Oman | #124 (WA) |
| *E. s. obliteratus* Hamilton | #125 (WA) |
| *E. similis* Oman | #126 (WA) |
| *E. s. confinis* Oman* | #126 (WA) |
| *E. s. dubiosus* Oman* | #59 (WA) |
| *E. s. kahlotus* Oman | #59 (WA) |
| *E. s. medialis* Oman | #109 (OR) |
| *E. s. minutus* Oman* | #109 (OR) |
| *E. s. nanus* Oman* | #109 (OR) |
| *E. s. relativus* Oman* | #126 (WA) |
| *E. s. sobrinus* Oman | #127 (WA) |
| *E. s. socius* Oman | #128 (WA) |
| *E. s. truncus* Oman* | #109 (OR) |
| *E. s. zonarius* Oman | #129 (WA) |
| *E. solus* Oman | #96 (MT) |
| *E. variabilis* Oman | #130 (WA) |
| *E. v. erratus* Hamilton | #110 (OR) |
| *E. v. gracilis* Hamilton | #111 (ID) |
| *E. v. mimicus* Hamilton | #112 (OR) |
| *E. wolfei* Oman | #131 (WA) |
| *E. winquatt* Oman | #113 (OR) |
| *Euscelis relativa* (Gill. & B.) | **northern** |
| *Evacanthus lacunar* Hamilton | #135 (OR) |
| *Flexamia decora* Beam. & T. | #12 (prairie) |
| *F. inflata* (Osborn & Ball) | prairie |
| *F. serrata* Beamer & Tuthill | prairie |

| | |
|---|---|
| *Frigartus frigidus* (Ball) | prairie |
| *Gyponana hasta* DeLong | southern |
| *Hardya dentata* (Osborn & B.) | prairie |
| *Hebecephalus abies* Hamilton | #153 (UT) |
| *H. caecus* Beamer | #60 (ID/OR) |
| *H. callidus* (Ball) | #61 (PNW) |
| *H. chandleri* Hamilton | #144 (WY) |
| *H. crassus* (DeLong) | #62 (BC/ ID-WY) |
| *H. crenulatus* Hamilton | #86 (ID) |
| *H. ferrumequinum* Hamilton | #87 (ID) |
| *H. filamentus* Hamilton & R. | #154 (ID) |
| *H. firmus* Beamer | #63 (WA/ MT-WY) |
| *H. hilaris* Beamer | #64 (WA/WY) |
| *H. occidentalis* Beamer & T. | prairie |
| *H. planaria* Hamilton | #79 (BC) |
| *H. picea* Hamilton | #88 (ID) |
| *H. pugnus* Hamilton | #89 (ID) |
| *H. rostratus* Beamer & Tut. | prairie |
| *H. sagittatus* Beamer & Tut. | #65 (PNW) |
| *H. truncatus* Beamer & Tut. | prairie |
| *H. veretillum* Hamilton | #90 (ID) |
| *H. vinculatus* Ball | #145 (CO) |
| *Hecalus montanus* (Ball) | **northern** |
| *H. viridis* (Uhler) | prairie |
| *Idiodonus heidemanni* (Ball) | #15 (southern) |
| *I. josea* (Ball) | #146 (CO/MT) |
| *Laevicephalus salarius* Knull | ? (BC/UT) |
| *Latalus curtus* Beamer & Tut. | #67 (PNW) |
| *L. histrionicus* Beirne | #49 (BC/AZ) |
| *L. intermedius* Ross & H. | #50 (PNW) |
| *L. missellus* (Ball) | **northern** |
| *L. mundus* Beamer & Tuthill | #68 (PNW) |
| *L. occidentalis* (DeLong) | #136 (OR) |
| *Lebradea flavovirens* (G. & B.) | **northern** |
| *Limotettix beameri* (Medler) | #137 (OR/WA) |
| *Limotettix bullatus* (Ball) | southern |
| *L. finitimus* (Van Duzee) | southern |
| *L. glomerosus* (Ball) | southern |
| *L. symphoricarpae* (Ball) | prairie |
| *L. zacki* Hamilton | #132 (WA) |
| *Lonatura salsura* (Ball) | prairie |
| *Lystridea uhleri* Baker | southern |
| *Mesamia frigida* (DeL. & H.) | southern |
| *M. ludovicia* Ball | #16 (prairie) |
| *Mocuellus caprillus* Ross & H. | #17 (prairie) |
| *M. c. anfractus* Hamilton | #91 (ID) |
| *M. c. strictus* Ross & H. | **northern** |
| *M. larrimeri* (DeLong) | #69 (PNW) |
| *M. quinquespinus* Hamilton | #155 (UT) |
| *Norvellina clarivida* (Van D.) | #18 (prairie) |
| *N. columbiana* (Ball) | prairie |
| *N. curvata* Lindsay | #156 (WY) |
| *N. perelegantis* (Ball) | southern |
| *N. rubida* (Ball) | #70 (PNW) |
| *N. saucia* (Ball) | #147 (CO) |
| *N. vermiculata* Lindsay | #71 (ID/CO) |
| *Orocastus hyalinus* (Beamer) | #148 (CO) |
| *O. labeculus* (DeLong) | #19 (prairie) |
| *O. pinnipenis* Ross & H. | #72 (ID-MT) |
| *O. perpusillus* (Ball & DeL.) | #20 (prairie) |
| *O. tener* (Beamer & Tuthill) | southern |
| *Paluda gladiola* (Ball) | **northern** |
| *Paraphlepsius lascivius* (Ball) | prairie |
| *P. occidentalis* (Baker) | southern |
| *Pinumius sexmaculatus* (Gillette & Baker) | #21 (prairie) |
| *Prairiana kansana* (Ball) | #22 (prairie) |
| *Psammotettix amplus* (D. & D. | southern |
| *P. attenuens* (DeLong & D.) | #73 (PNW) |
| *P. beirnei* Greene | #37 (BC) |
| *P. dentatus* Knull | southern |
| *P. diademata* Hamilton | #138 (BC) |
| *P. greenei* Hamilton | #114 (OR) |
| *P. lividellus* (Zetterstedt) | **northern** |
| *P. nesiotus* Hamilton | #139 (BC) |
| *P. obesus* Knull | southern |
| *P. shoshone* (DeLong & Dav.) | southern |
| *P. totalus* (DeLong & Dav.) | #23 (ID-MT-WY) |
| *P. viridinervis* Ross & H. | #149 (WY) |
| *Rosenus cruciatus* (Osborn & Ball) | #24 (prairie) |
| *R. decurvatus* Hamilton & R. | #80 (BC) |
| *R. obliquus* (DeLong & Dav.) | #92 (ID) |
| *Scaphytopius diabolus* (Van Duzee) | southern |
| *S. oregonensis* (Baker) | southern |
| *Sorhoanus bimaculatus* (Gillette & Baker) | **northern** |
| *S. debilis* (Uhler) | #51 (PNW) |
| *S. involutus* Hamilton | #150 (CO) |
| *S. uhleri* (Oman) | **northern** |
| *S. virilis* Hamilton | #52 (OR) |
| *S. xiphosura* Hamilton | #74 (PNW) |
| *Stenometopiellus vader* Ham. | #37 (ID-MT) |
| *Stragania atra* (Baker) | prairie |
| *S. rufoscutellata* (Baker) | prairie |
| *Texananus cumulatus* (Ball) | southern |
| *T. dolus* DeLong | prairie |
| *T. extremus* (Ball) | southern |
| *T. lathropi* (Baker) | southern |
| *T. latipex* (DeLong) | southern |
| *T. oregonus* (Ball) | southern |
| *T. proximus* Crowder | southern |
| *Twiningia fasciatus* (Beamer) | southern |
| *T. pellucidus* (Ball) | southern |
| *T. scrupulosus* (Ball) | southern |
| *Unoka dramatica* Hamilton | #39 (BC) |

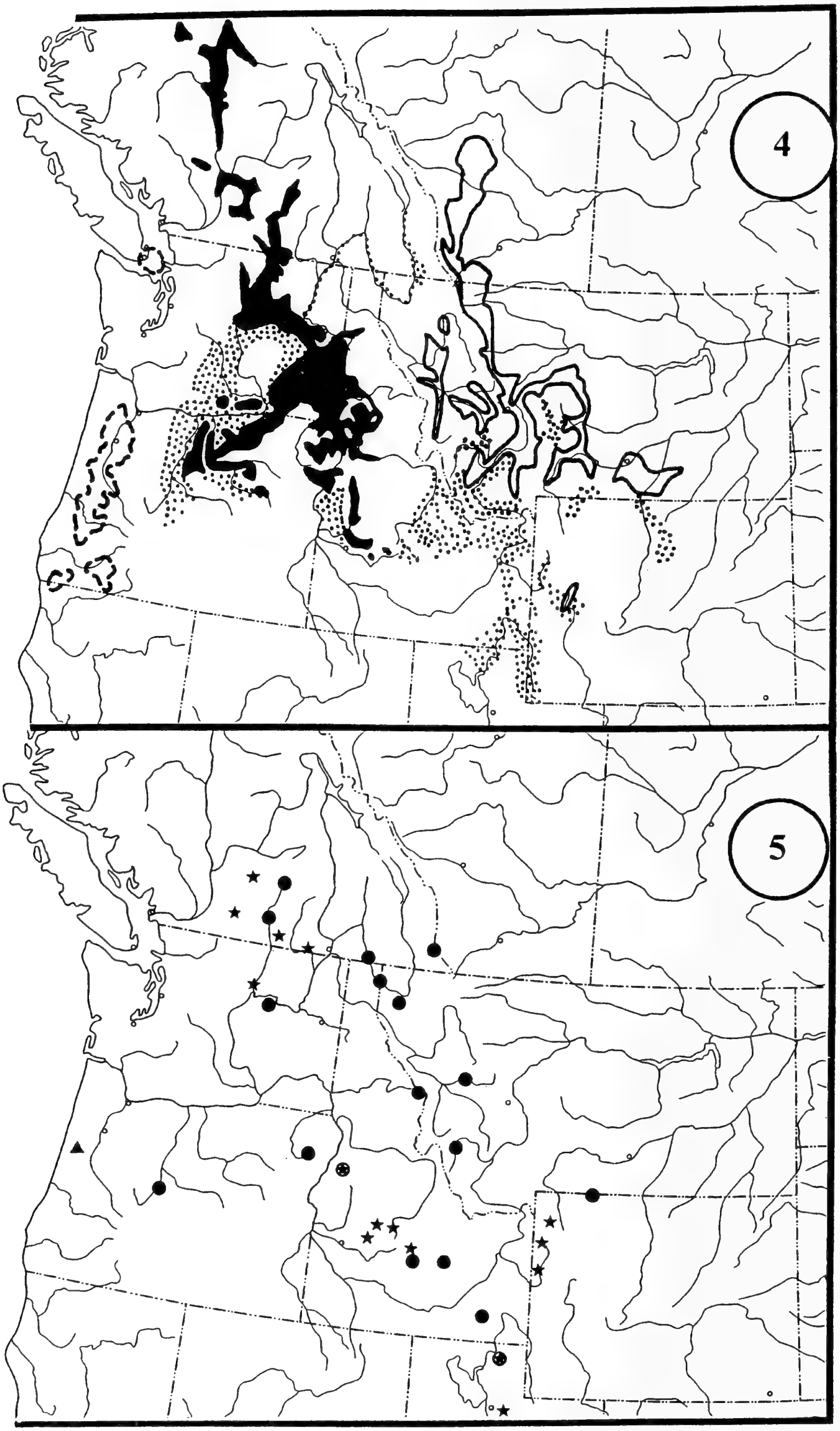
| | |
|---|---|
| *U. gillettei* Metcalf | #25 (prairie) |
| *Xerophloea zionis* Lawson | southern |

## DELPHACIDAE

| | |
|---|---|
| *Achorotile apicata* Hamilton | #157 (UT) |
| *Caenodelphax atridorsum* (Beamer) | #75 (MT/OR) |
| *Delphacodes anufrievi* Wils. | **northern** |
| *D. gillettei* (Van Duzee) | southern |
| *D. lineatipes* (Van Duzee) | **northern** |
| *D. neocclusa* Muir & Gifford | southern |
| *D. occlusa* (Van Duzee) | southern |
| *Elachodelphax mazama* Ham. | #40 (WA) |
| *E. pedaforma* (Beamer) | #27 (prairie) |
| *E. unita* Hamilton | #158 (UT) |
| *Eurybregma eurytion* Ham. | #41 (PNW) |
| *E. magnifrons* (Crawford) | #27 (PNW) |
| *Javesella lutulentella* (Muir & Gifford) | southern |
| *Kosswigianella irrutilo* Ham. | #151 (CO) |
| *K. wasatchi* Hamilton | #160 (UT) |
| *Laccocera canadensis* Beirne | #26 (prairie) |
| *L. flava* Crawford | #29 (prairie) |
| *Laccocera lineata* Scudder | prairie |
| *L. oregonensis* Penner | #42 (PNW) |
| *L. vanduzeei* Penner | #43 (PNW) |
| *L. vittipennis* Van Duzee | #30 (prairie) |
| *Megamelanus bicolor* Ball | southern |
| *Nothodelphax foveatus* (Van Duzee) | #31(prairie) |
| *N. glacia* Wilson | **northern** |
| *N. venustus* (Beamer) | #44 (PNW) |
| *Parkana alata* Beamer | southern |
| *Paraliburnia furcata* Hamilton | #81 (BC) |
| *P. kilmani* (Van Duzee) | **northern** |
| *P. lecartus* Hamilton | #82 (BC) |
| *Pissonotus frontalis* (Crawford) | southern |
| *P. rubrilatus* Morgan & B. | #76 (PNW) |
| *Prokelisia carolae* Wilson | southern |
| *P. salina* (Ball) | prairie |



**Figures 1-3.** Distribution of Pacific Northwest grasslands and widespread endemic leafhoppers. 1, provinces and states of the Pacific Northwest (boxed area); 2-3, geographical areas of PNW grasslands, with ID/MT border (box) enlarged to show Clark Fork valley system (shaded in Fig. 2, GA-GC in Fig. 3). Bold line: continental divide indicated by dividing area H (prairies) from areas F (Snake River plains) and G (Clark Fork valley); grey lines: county boundaries. For abbreviations, see text.



**Figures 4-5.** Distribution of types of PNW grasslands (4) and leafhoppers (5). Black, Palouse grasslands; stippled, grassland-sagebrush ecotone; outline, fescue grasslands; dashed outline, oak savannah; filled triangle, *Evacanthus lacunar* on Mary's Peak; filled circle, *Norvellina rubida*; star, *Sorhoanus xiphosura*.

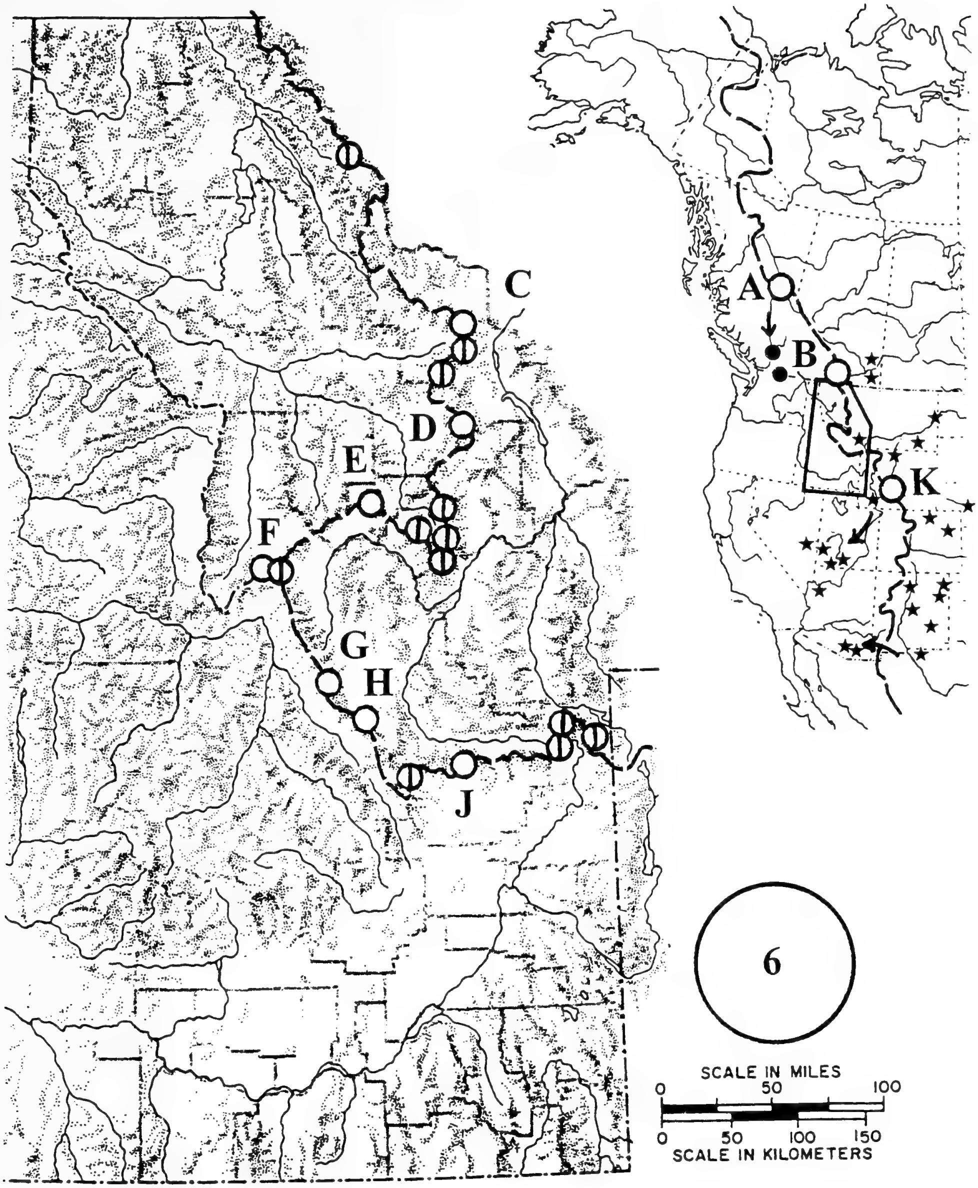


**Figure 6.** Distribution of *Unoka gillettei* (stars) and *U. dramatica* (filled circles) west of 101°W, showing invasion of montane area across Pacific continental divide (dashed line). Major passes from British Columbia to Wyoming (circles), from N to S: A, "Crooked River Pass," BC; B, Crowsnest Pass, BC/AB; *(continued in detail)* C, Rogers, MT (1800 m); D, MacDonald Pass; E, "Grassy Pass", MT; F, Lost Trail Pass, ID/MT; G-H, Lemhi and Bannock passes, ID/MT; J, Monida Pass, ID/MT; K, Great Basin Divide, WY. Open circles represent most important passes for leafhopper dispersal; split circles, other passes.

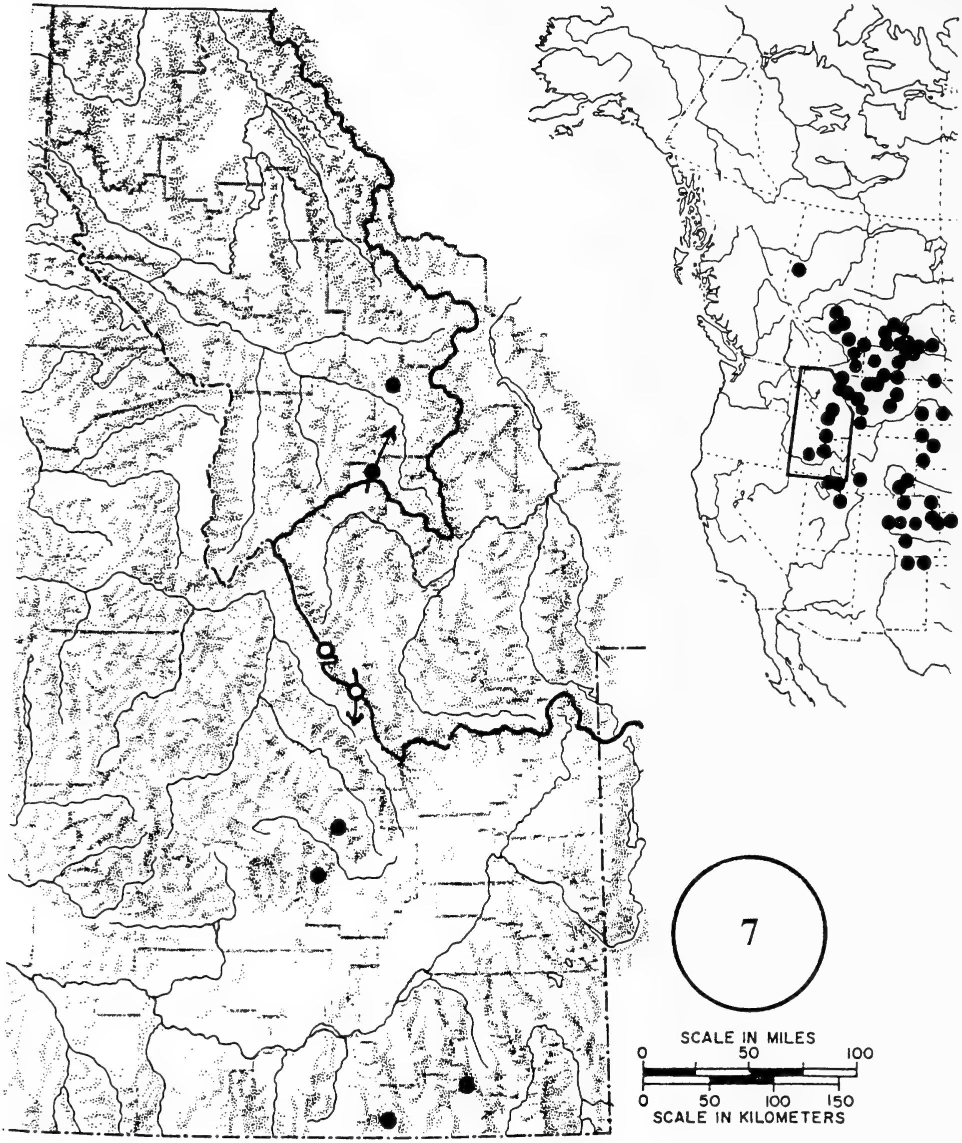


**Figure 7.** Distribution of the leafhopper *Athysanella attenuata* west of 101°W. Box, area of detail; solid line, continental divide; open circles, dispersal routes across Lemhi and Bannoch passes.

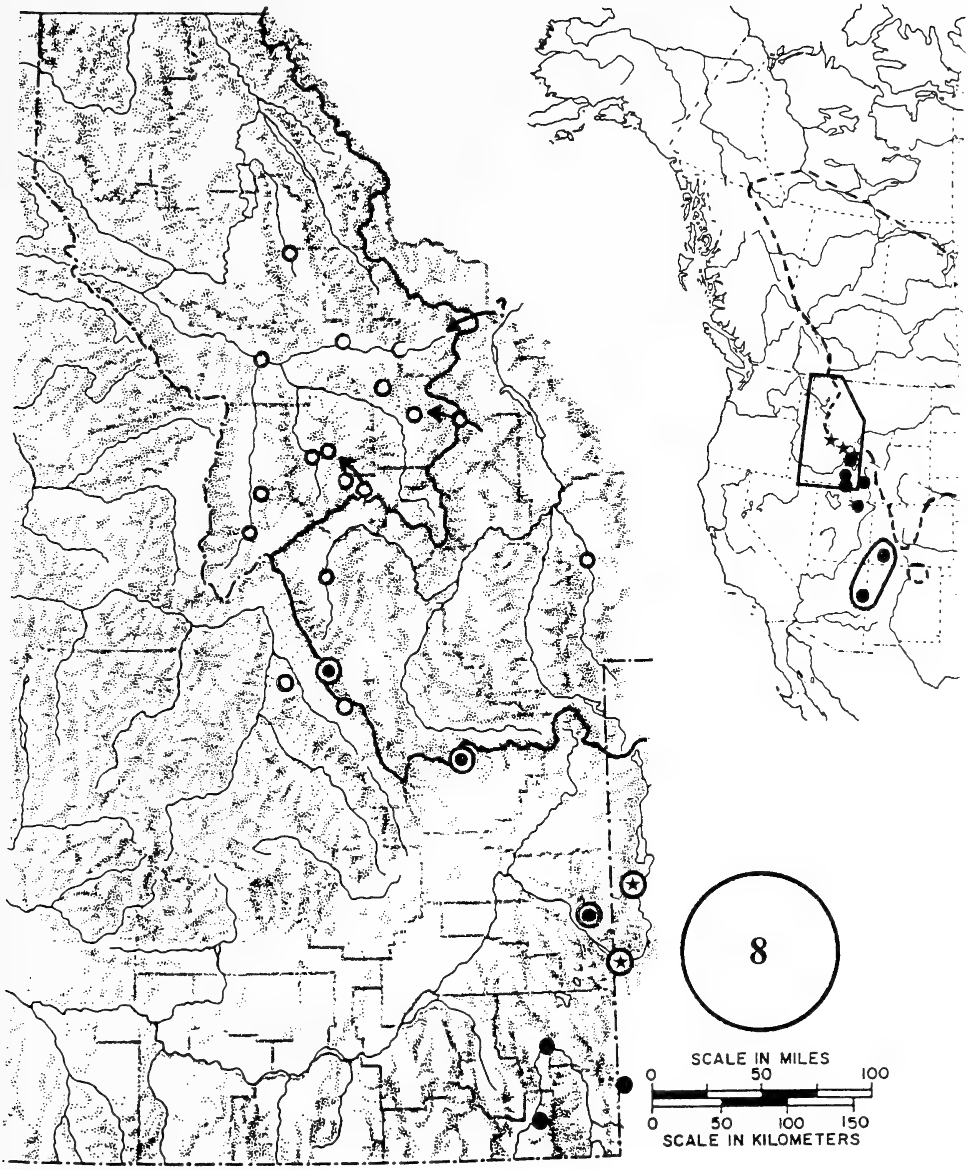


**Figure 8.** Distribution of the leafhoppers *Diplocolenus configuratus* (dashed line and open circle), *D. configuratus bicolor* (star) and *D. configuratus nigrior* (filled circle) west of 101°W. Box, area of detail; oval, populations confined to mountains; bull's eye, hybrid populations.

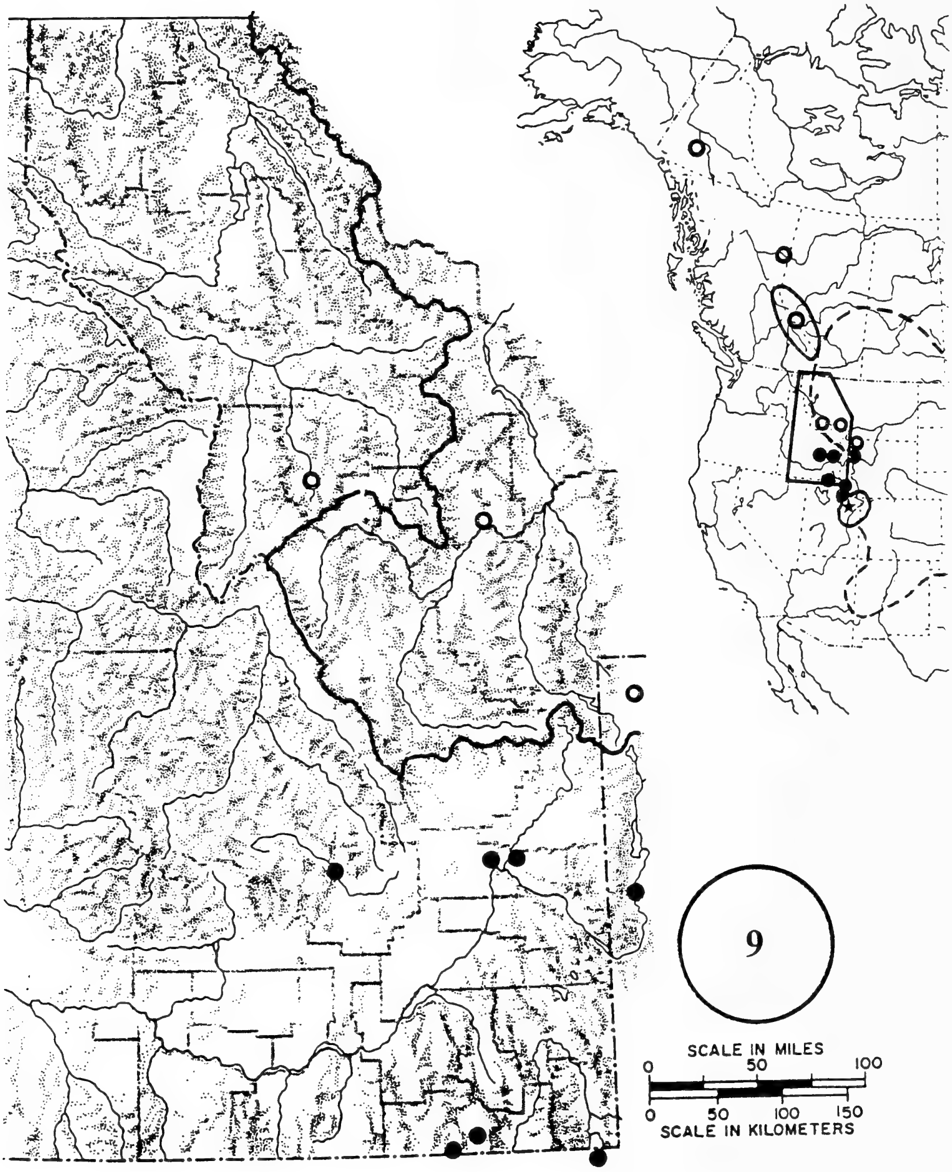


**Figure 9.** Distribution of the leafhoppers *Mocuellus quinquespinus* (star), *M. caprillus* (dashed line), *M. caprillus anfractus* (filled circles) and *M. caprillus strictus* (open circles). Box, area of detail; ovals, populations confined to mountains; arrows, inferred dispersal route across Lemhi and "Grassy Pass."

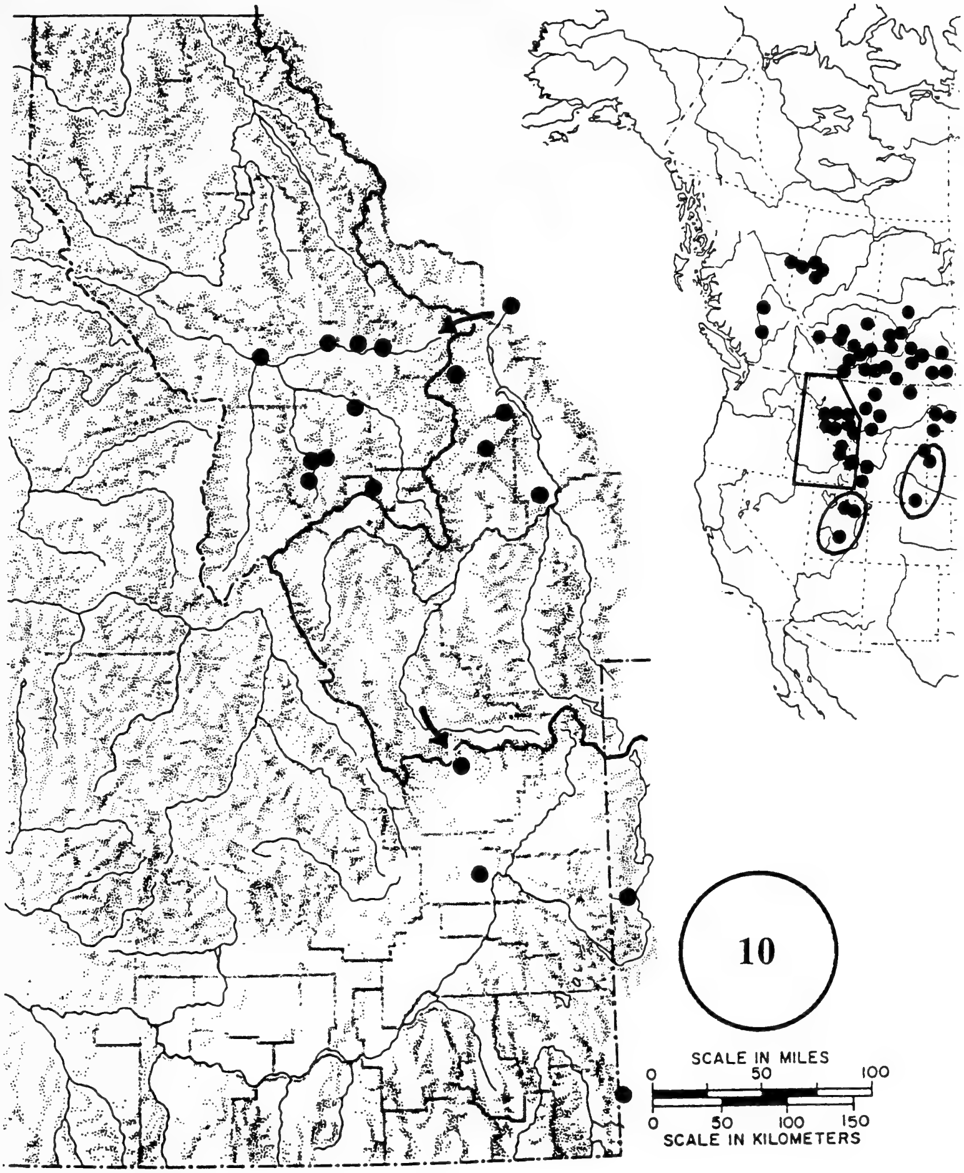


**Figure 10.** Distribution of the leafhopper *Orocastus perpusillus* west of 101°W. Box, area of detail; ovals: southern populations confined to mountains; arrows, inferred dispersal route across Rogers and Monida passes.

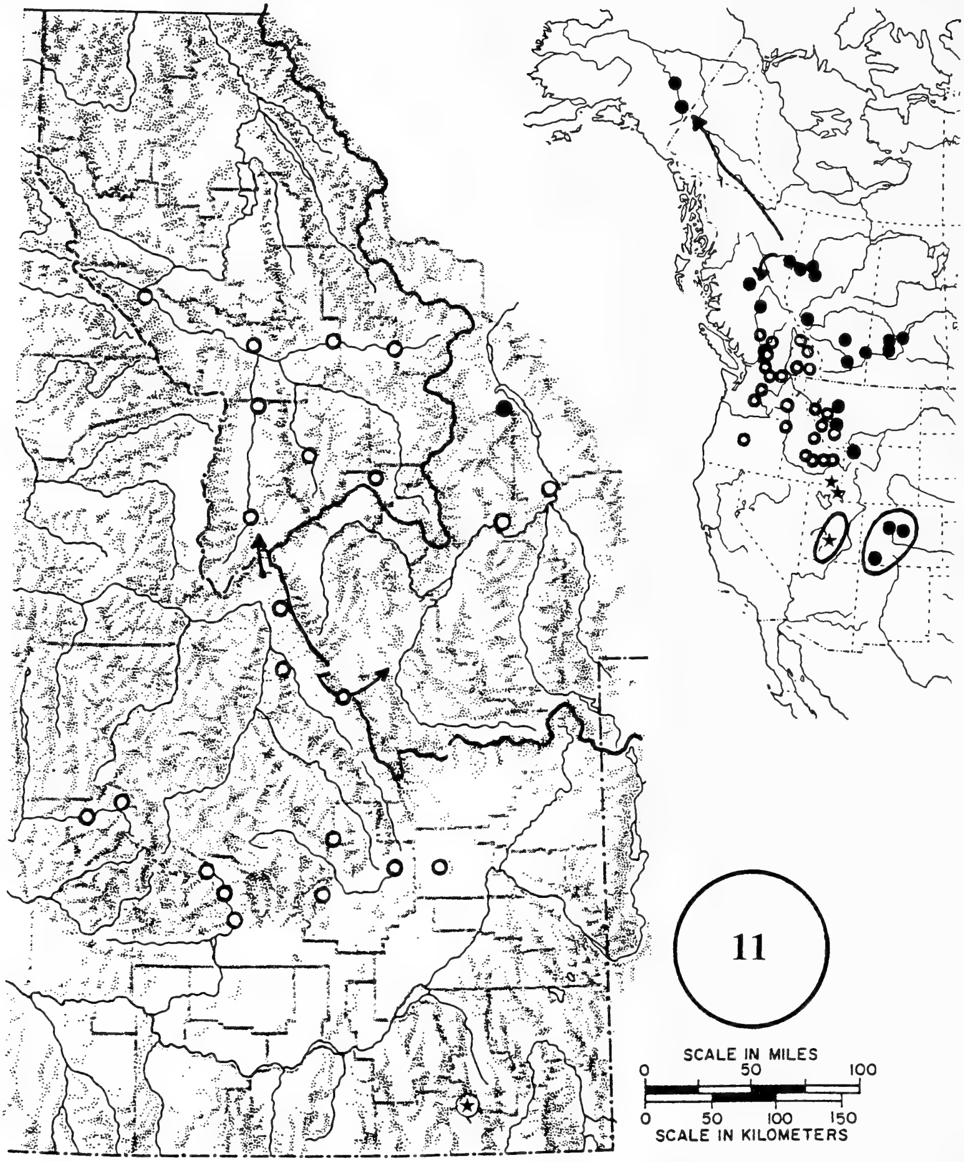


**Figure 11.** Distribution of the planthoppers *Eurybregma eurytion* (open circles) and *Eurybregma magnifrons* (filled circles). Ovals, populations confined to mountains; arrows, inferred dispersal routes.

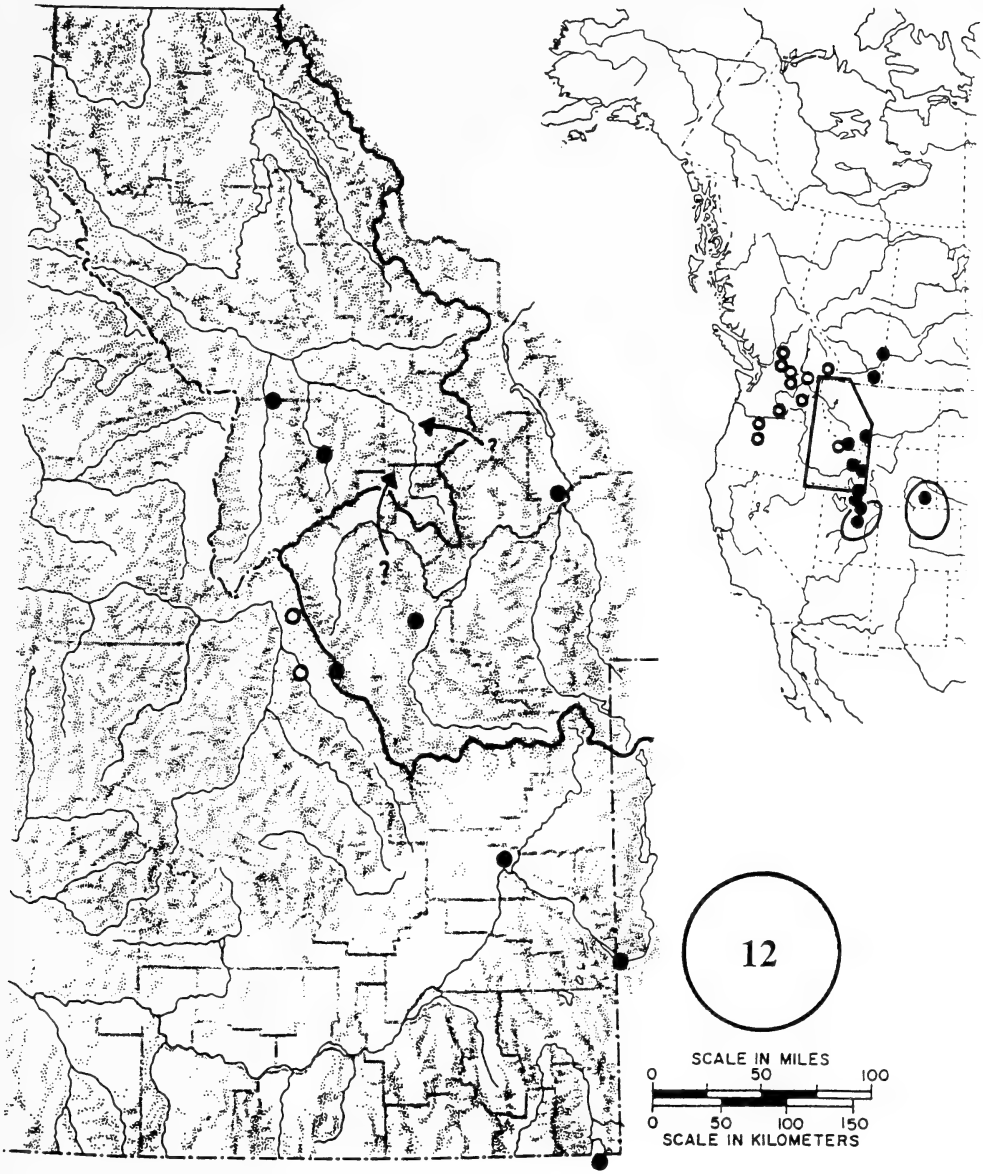


**Figure 12.** Distribution of the planthoppers *Laccocera oregonensis* (open circles) and *Laccocera flava* (filled circles). Box, area of detail; ovals, populations confined to mountains; arrows, inferred dispersal route across MacDonald or "Grassy Pass."

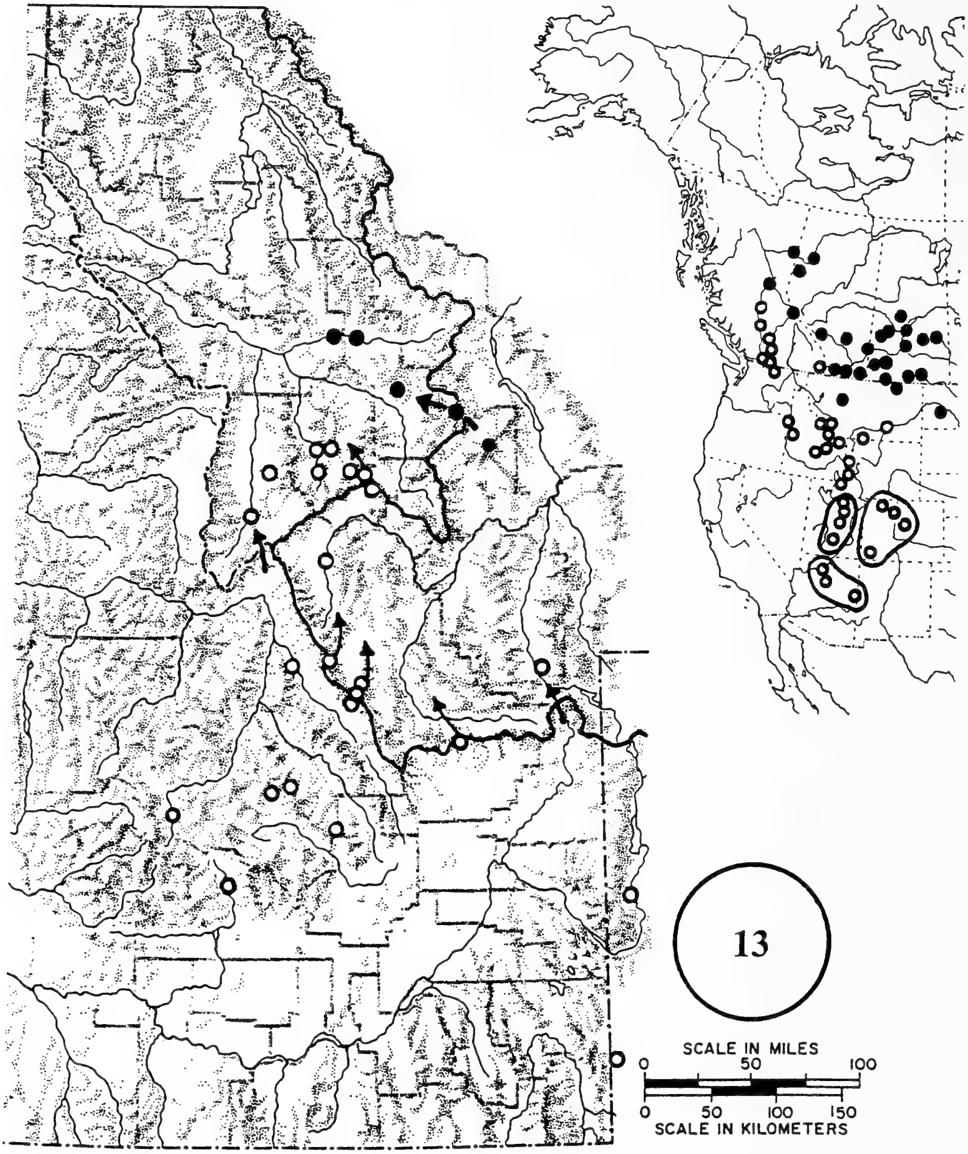


**Figure 13.** Distribution of the planthoppers *Laccocera* spp. (*vittipennis* group) west of 101°W. Open circles, *L. vanduzeei*; filled circles, *Laccocera vittipennis*; outlines, populations confined to mountains; arrows, inferred dispersal route across MacDonald, "Grassy Pass", Lost Trail, Lemhi, Bannock, Monida and Raynolds passes.

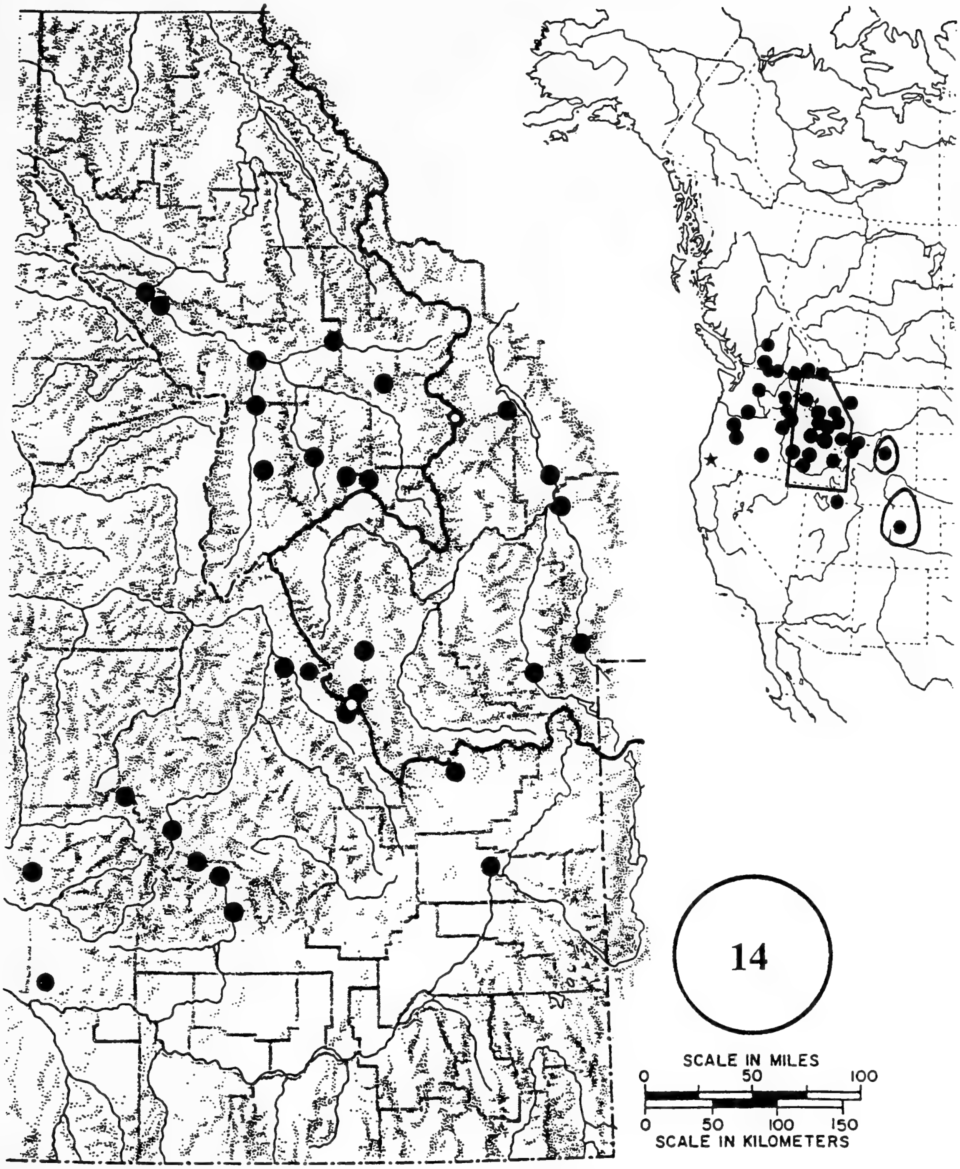


**Figure 14.** Distribution of the leafhoppers *Sorhoanus debilis* (circles) and *Sorhoanus virilis* (star). Box: area of detail; ovals: populations confined to mountains; open circle, sample from pass.

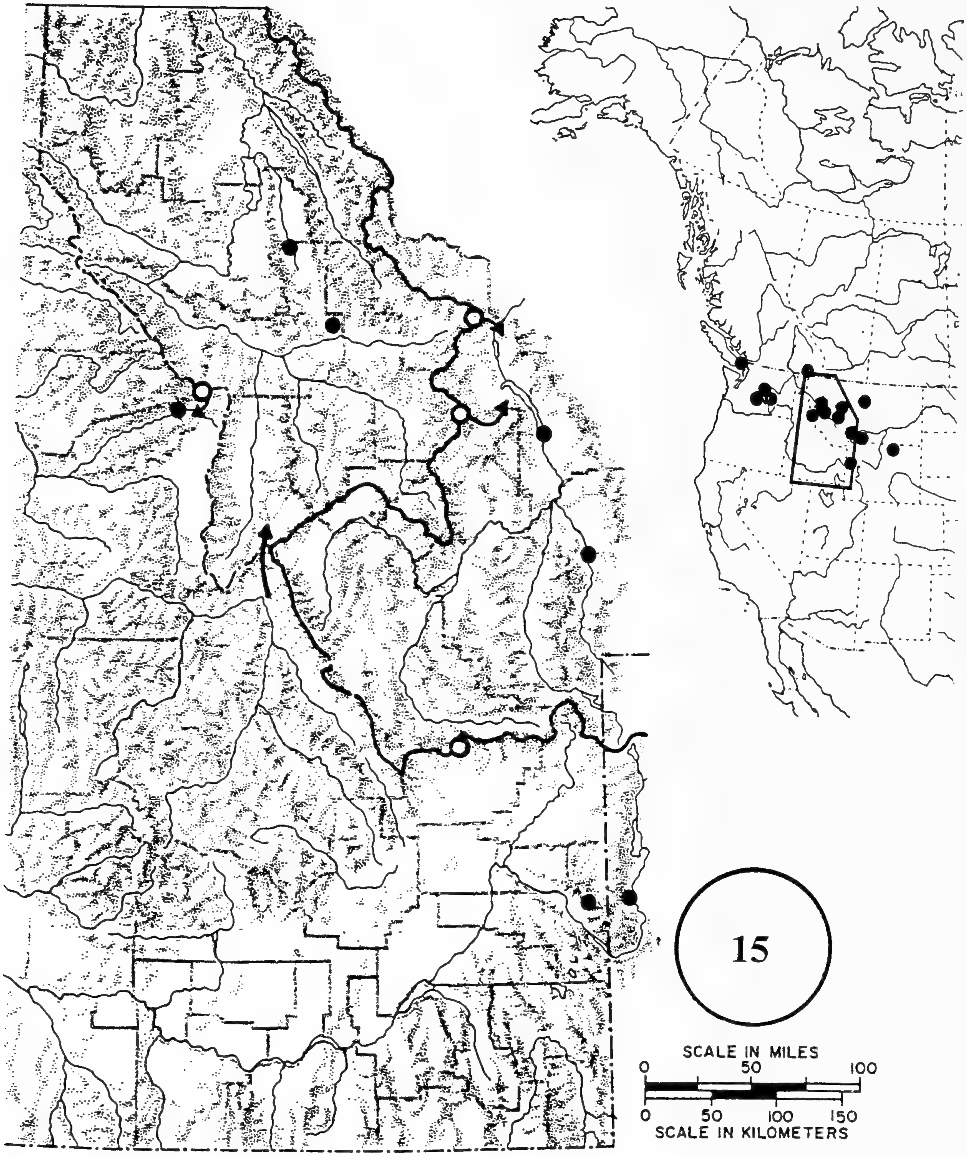


**Figure 15.** Distribution of the leafhopper *Endria montana*. Box, area of detail; arrows, inferred dispersal route across Lost Trail, Lolo, Rogers and MacDonald passes (open circles).

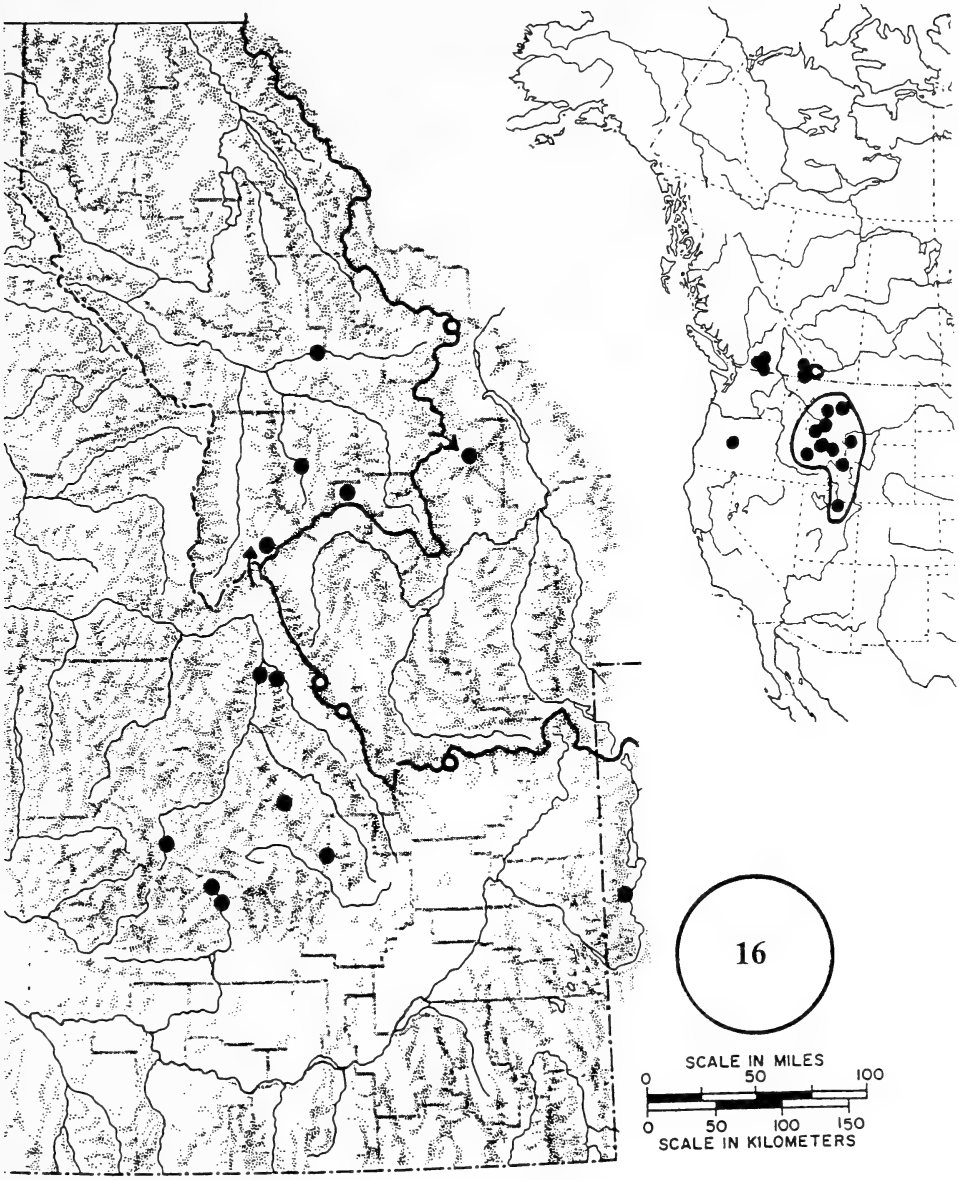


**Figure 16.** Distribution of the leafhopper *Orocastus pinnipenis*. Outline, eastern populations confined to mountains; open circles, taken in passes; arrows, inferred dispersal routes through Lost Trail and MacDonald passes.

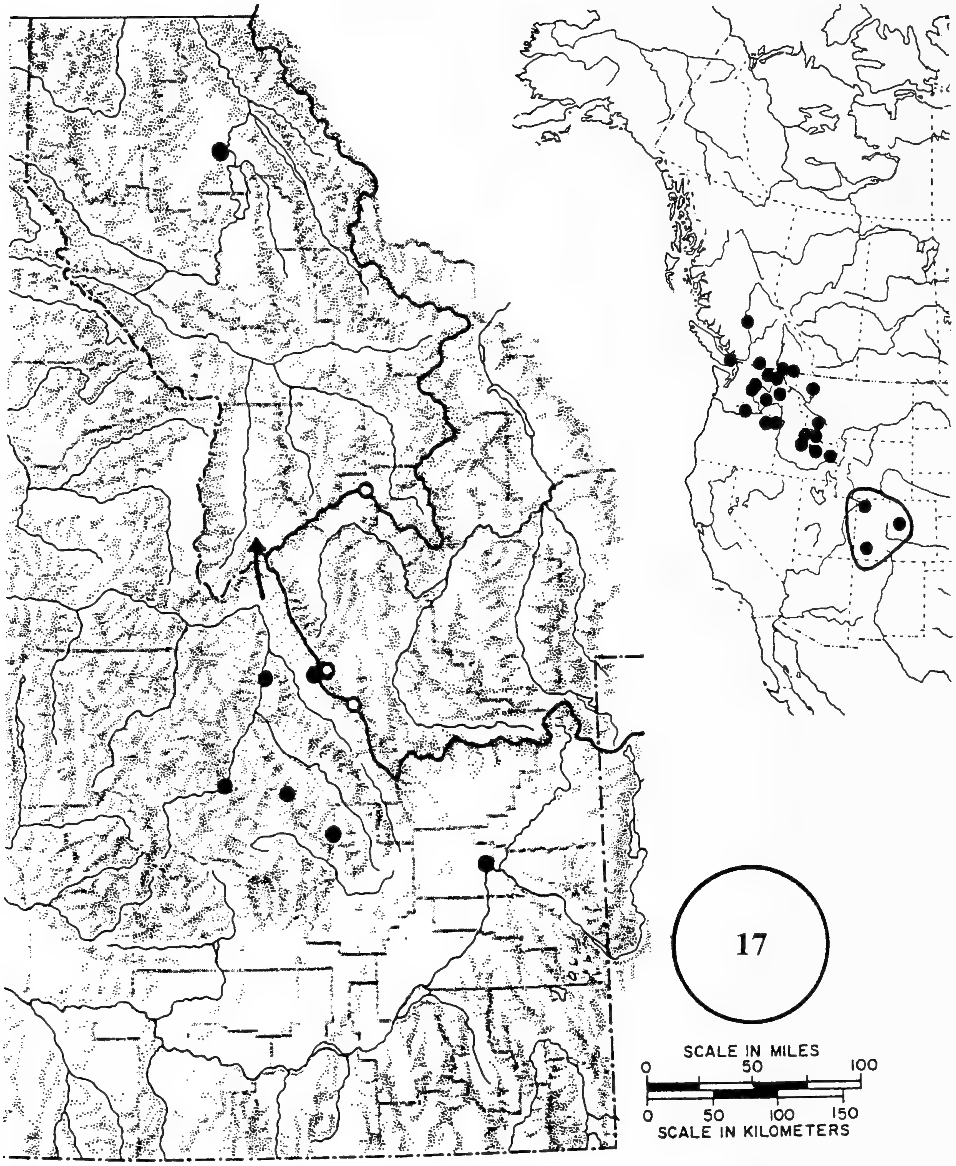


**Figure 17.** Distribution of the leafhopper *Psammotettix attenuens*. Outline, populations confined to mountains; open circles, samples taken in passes; arrow, inferred dispersal route through Lost Trail Pass.

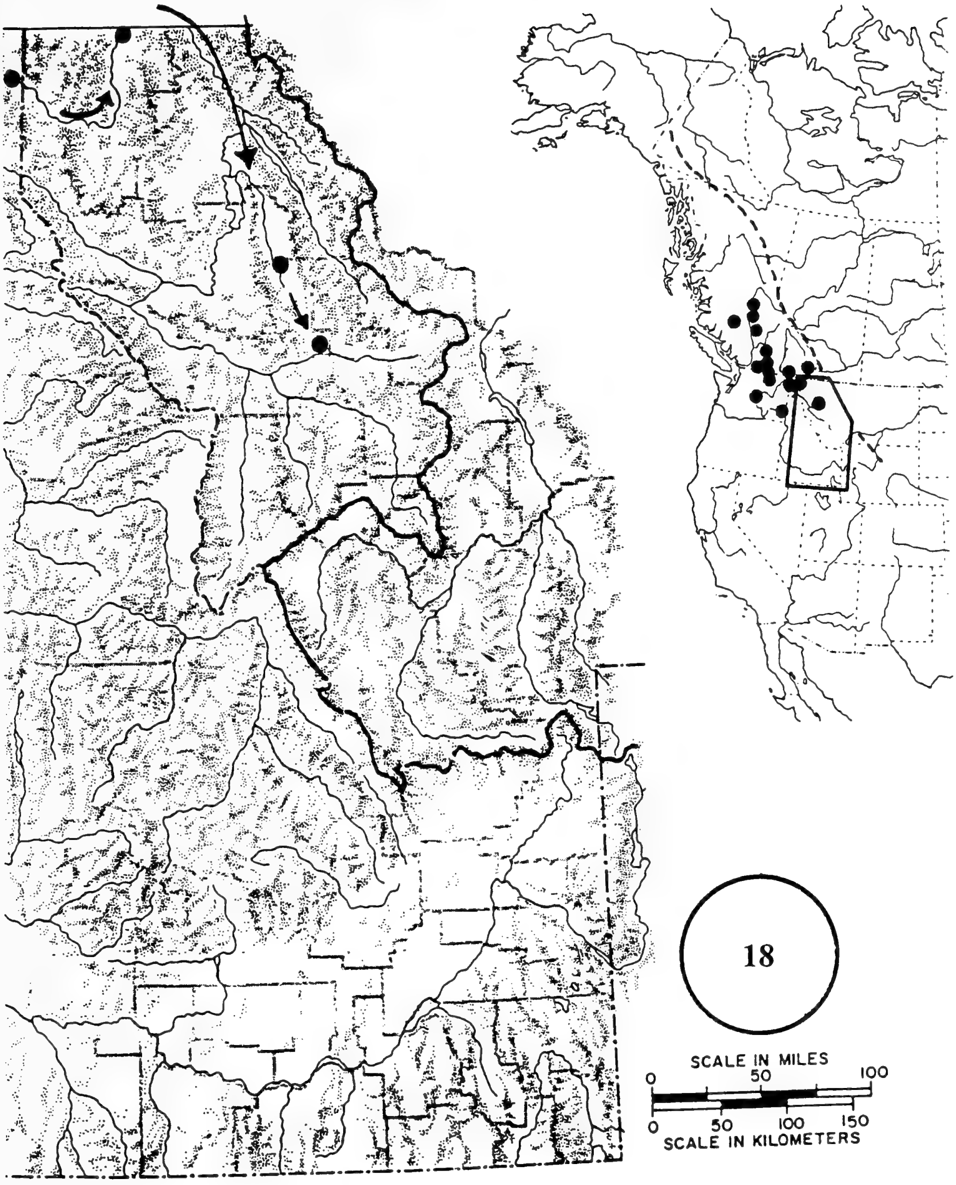
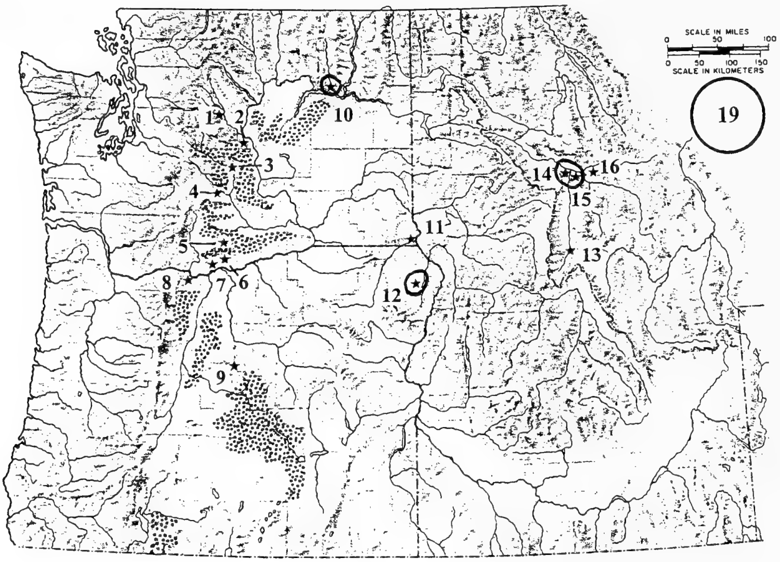


**Figure 18.** Distribution of the leafhopper *Cuerna* spp. west of 101°W. Box, area of detail; dashed line, western extent of *C. septentrionalis*; filled circle, *C. cuesta*; arrows, inferred dispersal route.

**Figure 19 (following page).** Distribution of glacial-age patterned ground (stippled) in the PNW and probable glacial refugia of relict populations of the flightless genus *Errhomus* (stars). 1, *E. picturatus*; 2, *E. serratus obliteratus*; 3, *E. reflexus*; 4, *E. serratus instabilis*; 5, *E. satus*; 6, *E. praedictus*; 7, *E. paradoxus*; 8, *E. winquatt*; 9, *E. ochoco*; 10, *E. calvus*; 11, *E. josephi*; 12, *E. pallidus*; 13, *E. bracatus*; 14, *E. rivalis*; 15, *E. solus*; 16, *E. camensis*. Circled: species that have shifted to non-balsamroot hosts. All species shown in modern sites, except for 3, 10, 11 and 15 which are shown with contracted ranges.



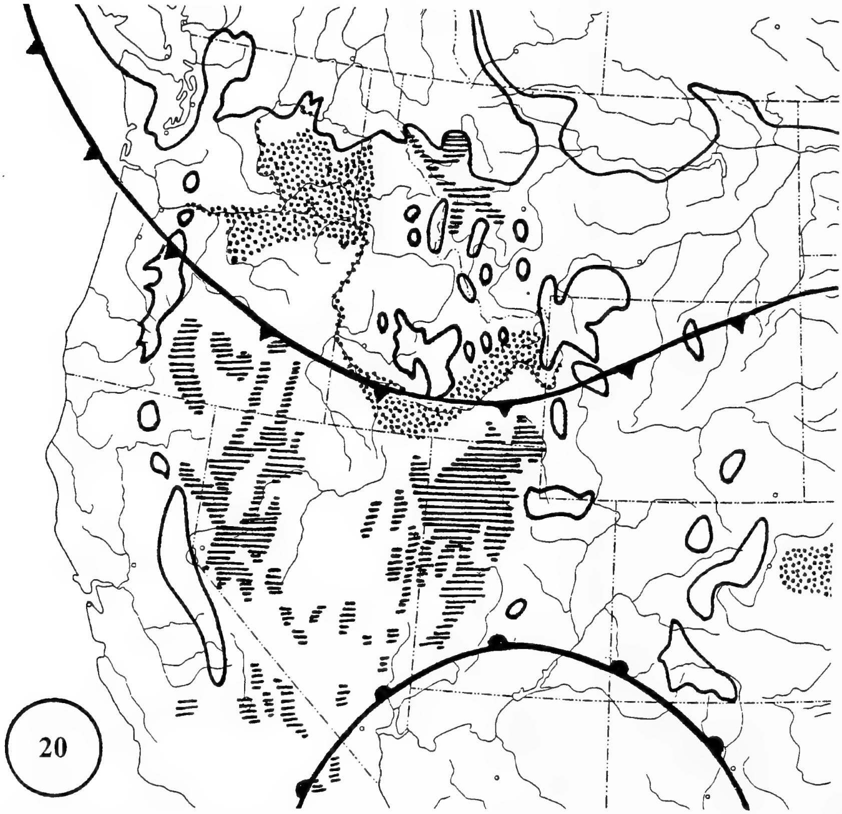


**Figure 20.** Hypothetical summer monsoon over PNW and areas to the south during the height of Pleistocene glaciation, showing permanent high pressure system (cold front) over WA, ID and MT and permanent low pressure system (warm front) over AZ; prevailing winds between these would be east to west (reverse of winter direction), bringing wetter than normal conditions to UT, NV and southern OR. Outline, ice cover; stippled, loess deposits and canyons; striped, glacial-age lakes.

# Occurrence of the spider mite predator *Stethorus punctillum* (Coleoptera: Coccinellidae) in the Pacific Northwest

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*Stethorus punctillum* Weise is a Palearctic species first reported in North America by Brown (1950), but found in the 1940's in collections from Ontario (Putman 1955). The beetle was collected on Lulu Island near Vancouver BC in 1950 (Tonks 1953). Since 1997 it has been mass reared and sold (Applied Bio-nomics Ltd., Saanich, BC) as a biological control agent for two-spotted spider mites, *Tetranychus urticae* Koch (Acari: Tetranychidae) (Raworth 2001).

According to Gordon (1985) *S. punctum picipes* Casey, a species native to North America, and the introduced species *S. punctillum* have overlapping distributions on the west coast of North America. Concern about the potential impact of commercial releases of *S. punctillum* on the species complex in the Lower Fraser Valley prompted a review of our recent collections of *Stethorus,* and collections of two other researchers, from the Pacific Northwest.

*Stethorus* spp. were collected during various studies from: raspberry, *Rubus idaeus* L. (Rosaceae) at Abbotsford BC (1986, 1996), Summerland BC (1997), and Snohomish and Skagit Counties WA (1991); corn, *Zea Mays* L. (Gramineae) at Vancouver BC (1992); and greenhouse cucumber *Cucumis sativus* L. (Cucurbitaceae) at Abbotsford (1995) and Cobble Hill BC (1996). The beetles were maintained in 70% ethanol and the genitalia of the males were dissected and mounted on slides. Identifications were based on Gordon (1985) using a phase contrast microscope, and confirmed by Y. Bousquet at the Eastern Cereal and Oilseed Research Centre, Ottawa. Forty-three male beetles collected from the Pacific Northwest were all *S. punctillum*. Five male beetles collected from Summerland, BC were all *S. punctum picipes*.

*Stethorus punctillum* was the only species found in collections from agricultural habitats in the Pacific Northwest during a 12-year period. Although the sample size was not large (43 males), the samples were consistent among years and locations, suggesting that *S. punctillum* is the dominant species. Continued inundative and augmentative releases of *S. punctillum* will probably not alter the species complex in the Lower Fraser Valley. *Stethorus punctillum* may have displaced *S. punctum picipes* in agricultural areas of Vancouver Island and the Lower Fraser Valley prior to commercial releases. Putman (1955) described a rapid displacement in southern Ontario between 1930 and 1940. No mass reared beetles have as yet been distributed to growers in the Okanagan Valley, although 500 have been sold to a grower further east, at Winlaw (Bob Macadam, Westgro Sales Inc., personal communication). Further work is needed to determine the nature of the complex in the Okanagan.

## ACKNOWLEDGEMENTS

The authors thank B. Congdon and D. Gillespie for additional samples of *Stethorus*, and Y. Bousquet for confirming our identifications. The work was funded in part by the BC Raspberry Growers' Association, the BC Greenhouse Vegetable Research Council and the Federal MII and PERD programs. Pacific Agri-Food Research Centre, Agassiz contribution no. 677.

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# Species of Alaska Scolytidae: Distribution, hosts, and historical review

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## ABSTRACT

The species of Scolytidae in Alaska have not been compiled in recent times although many of them are included in earlier broader works. The authors of these works are summarized in a brief history of forest entomologists in Alaska. Fifty-four species of Alaskan Scolytidae are listed (23 species in the subfamily Hylesininae and 31 in the subfamily Scolytinae) belonging to 24 genera (11 in Hylesininae and 13 in Scolytinae). They infest 15 species of trees and shrubs of which 10 are conifers (host to 48 species of Scolytidae) and 5 are angiosperms (host to 6 species of Scolytidae). Fifty species are bark beetles that inhabit phloem and four species are ambrosia beetles that live in sapwood. All are species native to Alaska.

**Keywords:** Bark beetles, Scolytidae, conifers, angiosperms, Alaska

## INTRODUCTION

The biographic regions of Alaska reflect the great expanse of that state, extending over a wide range of latitude, longitude, and elevation. In broad terms, these regions are characterized by a relatively mild and moist coastal climate, particularly in the southeast and coastal south-central areas; an extensive drier, colder climate in interior and northern Alaska; and numerous mountain ranges that attain the highest elevation on the continent.

Except for willows (*Salix* spp.), the species of Alaskan trees are somewhat more diverse in the coastal environment. Because species of Scolytidae are host-specific to a marked degree, the extent of their diversity generally reflects that of woody plant species that are needed and available for their existence. Warmer climate also enhances scolytid diversity by exerting less selective pressure as is evident in tropical regions. Thus, more than half of the known Alaskan scolytid fauna occur in rather close proximity to the coast. Nonetheless, white spruce, *Picea glauca* (Moench) Voss, a tree that occurs widely in the interior, is host of more species of scolytids than any other tree species in Alaska (Table 1).

The species of Scolytidae in Alaska have not been compiled in recent times although many of them are included in the broader works of Bright (1976, 1981), and Wood (1982). The first record of Alaskan Scolytidae (12 species) was reported by C. G. Mannerheim in the period 1843-1853 (Hamilton 1894). Beckwith (1972) listed 17 species infesting spruce (*Picea* spp.), two of which have been placed in synonymy by Wood (1982). Werner and

Holsten (1984) listed 29 species attracted to pheromone baited traps and spruce trap trees. Werner (2002) lists 23 species in relation to various environmental disturbances in interior Alaska white spruce forests. Gara et al. (1995) list 12 scolytid species associated with the spruce beetle, *Dendroctonus rufipennis* (Kirby), in white and Lutz spruce (*Picea* x *lutzii* Little). The biology of the more common scolytids of Alaska is described by Holsten *et al.* (2001). Records of some secondary scolytids are obscure, being mentioned rather incidentally in studies of more prominent primary species (e.g., Baker *et al.* 1977; Furniss *et al.* 1976, 1979; Werner 1986; Werner *et al.* 1977, 1981). This work draws together published and unpublished records since 1946. For perspective, a brief history is presented of the location and staffing of forest entomologists in Alaska.

## Table 1

Hosts of Alaskan Scolytidae.

| **Species of Scolytidae** | *Chamaecyparis nootkatensis* | *Picea glauca* | *Picea* x *lutzii* | *Picea mariana* | *Picea sitchensis* | *Pinus contorta* | *Larix laricina* | *Thuja plicata* | *Tsuga heterophylla* | *Tsuga mertensiana* | *Alnus* sp. | *Betula papyrifera* | *Populus tremuloides* | *Salix alaxensis* | *Salix scouleriana* | *Salix* sp |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Hylesininae** | | | | | | | | | | | | | | | | |
| *Alniphagus aspericollis* | | | | | | | | | | | x | | | | | |
| *Carphoborus andersoni* | | x | | | | | | | | | | | | | | |
| *Carphoborus carri* | | x | | | | | | | | | | | | | | |
| *Carphoborus intermedius* | | x | | | | | | | | | | | | | | |
| *Dendroctonus punctatus* | | x | | | | | | | | | | | | | | |
| *Dendroctonus rufipennis* | | x | x | | x | | | | | | | | | | | |
| *Dendroctonus simplex* | | | | | | | x | | | | | | | | | |
| *Hylastes nigrinus* | | | | | | | | | | | | | | | | |
| *Hylurgops rugipennis rugipennis* | | | | | x | x | | | | | | | | | | |
| *Phloeosinus cupressi* | x | | | x | | | | | | | | | | | | |
| *Phloeosinus pini* | | x | | | | | | | | | | | | | | |
| *Phloeosinus punctatus* | | | | | | | | x | | | | | | | | |
| *Phloeotribus lecontei* | | x | | | | | | | | | | | | | | |
| *Phloeotribus piceae* | | x | | | | | | | | | | | | | | |
| *Polygraphus rufipennis* | | x | x | | x | x | | | | | | | | | | |
| *Polygraphus convexifrons* | | x | x | | | | | | | | | | | | | |
| *Pseudohylesinus granulatus* | | | | | | | | | | | | | | | | |
| *Pseudohylesinus sericeus* | | | | | | | | | | | | | | | | |
| *Pseudohylesinus sitchensis* | | | | x | x | | | | | | | | | | | |
| *Pseudohylesinus tsugae* | | | | | | | | | x | | | | | | | |
| *Scierus annectens* | | x | | | | | | | | | | | | | | |
| *Scierus pubescens* | | x | | | | | | | | | | | | | | |
| *Xylechinus montanus* | | x | | | | | | | | | | | | | | |
| **Scolytinae** | | | | | | | | | | | | | | | | |
| *Cryphalus pubescens* | | x | | | | | | | | | | | | | | |
| *Cryphalus ruficollis ruficollis* | | x | | | | | | | | | | | | | | |
| *Crypturgus borealis* | | x | | | x | | | | | | | | | | | |
| *Dolurgus pumilus* | | x | | | | | | | x | | | | | | | |
| *Dryocoetes affaber* | | x | x | | x | x | | | | | | | | | | |
| *Dryocoetes autographus* | | x | | | x | | | | x | | | | | | | |
| *Dryocoetes caryi* | | | x | | | | | | | | | | | | | |
| *Ips borealis borealis* | | x | x | | | | | | | | | | | | | |

| **Species of Scolytidae** | *Chamaecyparis nootkatensis* | *Picea glauca* | *Picea* x *lutzii* | *Picea mariana* | *Picea sitchensis* | *Pinus contorta* | *Larix laricina* | *Thuja plicata* | *Tsuga heterophylla* | *Tsuga mertensiana* | *Alnus* sp. | *Betula papyrifera* | *Populus tremuloides* | *Salix alaxensis* | *Salix scouleriana* | *Salix* sp |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Ips concinnus* | | | | | x | | | | | | | | | | | |
| *Ips perturbatus* | | x | | | | | | | | | | | | | | |
| *Ips pini* | | | | | | x | | | | | | | | | | |
| *Ips tridens* | | x | x | | x | | | | | | | | | | | |
| *Lymantor alaskanus* | | | | | | | | | | | | | | | | |
| *Orthotomicus caelatus* | | x | | | x | x | | | | | | | | | | |
| *Pityophthorus bassetti* | | x | | | | | | | | | | | | | | |
| *Pityophthorus carinulatus* Sw. | | | | | | x | | | | | | | | | | |
| *Pityophthorus murrayanae* | | x | x | | | | | | | | | | | | | |
| *Pityophthorus nitidulus* | | x | x | x | x | | | | | | | | | | | |
| *Pityophthorus nitidus* | | x | x | | | | | | | | | | | | | |
| *Pityophthorus opaculus* | | x | x | | | | | | | | | | | | | |
| *Pityophthorus recens* | | | x | | | | | | | | | | | | | |
| *Pityophthorus tuberculatus* | | | | | | x | | | | | | | | | | |
| *Procryphalus mucronatus* | | | | | | | | | | | | | x | | | |
| *Procryphalus utahensis* | | | | | | | | | | | | | | | x | x |
| *Pseudips* (=*Ips*) *mexicanus* | | | | | | x | | | | | | | | | | |
| *Scolytus piceae* | | x | | | | | x | | | | | | | | | |
| *Trypodendron betulae* | | | | | | | | | | | | x | | | | |
| *Trypodendron lineatum* | | x | | | x | | | | x | | | | | | | |
| *Trypodendron retusum* | | | | | | | | | | | | x | x | | | |
| *Trypodendron rufitarsus* | | x | | | | | | | | x | | | | | | |
| *Trypophloeus striatulus* | | | | | | | | | | | | | | x | | |

## HISTORY OF BARK BEETLE SURVEYS IN ALASKA

After Mannerheim's early work (Hamilton 1894), infestations of Alaskan bark beetles were reported only sporadically beginning in 1922 (Zogas and Holsten 2002). Forest entomologists were not directly involved until 1946 when Robert L. Furniss of the Portland, Oregon, Forest Insect Laboratory was requested by regional forester, B. Frank Heintzleman, to investigate dying Sitka spruce, *Picea sitchensis* (Bong.) Carr., on the Tongass and Chugach National Forests (Furniss 1946, 1948, 1950; Furniss and Jones 1946). William F. McCambridge was the first forest entomologist to be stationed in Alaska (Juneau, 1952-1956). He was replaced by George L. Downing; others have followed there to this time. Since 1976, Forest Service Alaska Region entomologists have also been stationed at Anchorage but mainly concerned with spruce beetle infestations on the Kenai Peninsula. Richard A. (Skeeter) Werner was stationed at the Institute of Northern Forestry at Fairbanks from 1974 until that facility closed in 1996. During that time, the Alaska State Division of Forestry hired entomologist Roger E. Burnside who is stationed at Anchorage.

## MATERIALS AND METHODS

Records of Alaskan species of Scolytidae were obtained from specimens available to us, from reviewers credited in Acknowledgments, and from the literature, including reports listed by Zogas and Holsten (2002). Such reports are on file at USDA, Forest Service, Alaska Region, Anchorage. Sources of specimens, locality information, and host data were primarily the Forest Service Alaska Region collections located at Anchorage and Juneau, and the senior author's collections. His specimens were collected during various studies and recreational visits since 1967 throughout all regions of the state where scolytids occur. Specimens are deposited at the USDA Forest Service, Alaska Region, in Anchorage and Juneau; in the W.F. Barr Entomological Museum, University of Idaho, Moscow, ID; Canadian National Collection of Insects, Arachnids and Nematodes (CNC), Ottawa; Brigham Young University, Provo, UT; Oregon State University, Corvallis, OR; and USDA, Agriculture Research Service, Beltsville, MD.

## RESULTS AND DISCUSSION

Fifty-four species of Alaskan Scolytidae are listed here (23 species in the subfamily Hylesininae and 31 in the subfamily Scolytinae). They belong to 24 genera (11 in Hylesininae and 13 in Scolytinae). They infest 15 species of Alaskan trees and shrubs of which 10 are conifers (host to 48 species of Scolytidae) and five are angiosperms (host to six species of Scolytidae). Fifty species are bark beetles that inhabit phloem and four species are ambrosia beetles that live in sapwood. All are native to Alaska. Four species new to Alaska are: *Phloeotribus lecontei* Schedl, *Cryphalus pubescens* Hopk., *Pityophthorus recens* Bright, and *Trypodendron betulae* Sw.

The following list is ordered alphabetically within each subfamily. Distributions include place names that may be found on road maps and in Orth (1967). For some species such as the spruce beetle we have found it more expedient to describe the extent of their occurrence in general terms. Where relevant, a remark is inserted to call attention to some aspect of a record. Such is the case with *Lymantor alaskanus* Wood for which the host is unknown. In this way we hope to stimulate additional collecting and study. Also, selected references are provided where available.

### Hylesininae

*Alniphagus aspericollis* (LeC.)
  Distribution: Hollis, Prince of Wales Is.
  Host: *Alnus* sp.
*Carphoborus andersoni* (Sw.)
  Distribution: Bonanza Cr. (nr. Fairbanks), Copper Center, Fort Yukon, John R., Salmon R., Sheenjek R.
  Host: *Picea glauca.*
*Carphoborus carri* Sw.
  Distribution: Bonanza Cr. (nr. Fairbanks), John R.
  Host: *Picea glauca.*
*Carphoborus intermedius* Wood
  Distribution: Bonanza Cr. (nr. Fairbanks).
  Host: *Picea glauca.*
*Dendroctonus punctatus* LeC.
  Distribution: Interior drainages. (Furniss 1995)
  Host: In the base of living *Picea glauca.*
*Dendroctonus rufipennis* (Kirby)
  Distribution: Throughout the distribution of its hosts. This is by far the most economically important scolytid in Alaska.
  Hosts: *Picea sitchensis, P. glauca, P.* x *lutzii and P. mariana.*
*Dendroctonus simplex* LeC.
  Distribution: Interior, throughout distribution of its host in the middle Yukon R. and in the Tanana R. drainage.

Host: *Larix laricina.*

*Hylastes nigrinus* (Mannerheim)

Distribution: Sitka Is.

Remarks: Holotype female in Helsinki Museum (Wood 1982), host not specified.

*Hylurgops rugipennis rugipennis* (Mannerheim)

Distribution: Farragut Bay, Ft. Yukon, Juneau, Kethikan, Kodiak Is., Loring, Sitka, Skagway.

Hosts: *Picea sitchensis, Pinus contorta.*

*Hylurgops subcostulatus subcostulatus* (Mannerheim)

Distribution: Kenai Penin.

Remarks: Holotype presumably lost (Wood 1982).

*Phloeosinus cupressi* (Hopk.)

Distribution: Chichagof Is., Juneau, Petersburg, Wrangell.

Host: *Chamaecyparis nootkatensis.*

*Phloeosinus pini* Sw.

Distribution: Bonanza Cr. (nr. Fairbanks), Chichagof Is., Eagle, Fairbanks, John R.

Host: *Picea glauca, Pinus contorta.*

*Phloeosinus punctatus* LeConte

Distribution: Edna Bay, Hollis, Kosciusko Is., Petersburg.

Host: *Thuja plicata.*

*Phloeotribus lecontei* Schedl

Distribution: Sheenjek R., Bonanza Cr. (nr. Fairbanks).

Host: *Picea glauca.*

Remarks: New state record.

*Phloeotribus piceae* Sw.

Distribution: Bonanza Cr. (nr. Fairbanks), Eagle R., Hope, John R., Summit L. (Kenai Penin.).

Host: *Picea glauca.*

*Polygraphus convexifrons* Wood

Distribution: Arviriaq, Bonanza Cr., John R., Matanuska, McKinley N.P., Noatak R., Quartz Cr. and Summit L. (Kenai Penin.), Walker L.

Hosts: *Picea glauca, P. x lutzii.*

*Polygraphus rufipennis* (Kby.)

Distribution: Anchorage, Bonanza Cr. (nr. Fairbanks), Bullfrog Is. (Yukon R.), Chandalar, Douglas, Dry Gulch and Cooper Landing (Kenai Penin.), Fairbanks, Ft. Yukon, Juneau, Klutina L., Homer, Hughes, John R., Kasilof, Kenai National Moose Range, Lawing (Kenai Lk.), McKinley, Mile 34 Seward Hwy., Montana Cr. (Mat-Su Valley), Moose Pass, Northway Jct., Russian R. (Kenai Penin.), Sheenjek R., Skilak L., Summit L.(Kenai Penin.), Talkeetna.

Hosts: *Picea glauca, P.* x *lutzii, P. mariana, P. sitchensis, Pinus contorta.*

*Pseudohylesinus granulatus* (LeConte)

Distribution: “Nauacin” (Wood 1982).

Host: Not specified, presumably *Tsuga heterophylla.*

*Pseudohylesinus sericeus* (Mannerheim)

Distribution: “Sitka” (Wood 1982).

Host: Not specified, presumably *Tsuga heterophylla.*

*Pseudohylesinus sitchensis* Sw.

Distribution: Kodiak Is., Juneau, Prince of Wales Is.

Host: *Picea sitchensis.*

*Pseudohylesinus tsugae* (Sw.)
Distribution: Chichagof Is., Dry Gulch (Kenai Penin.), Echo Cove (nr. Juneau), Glacier Highway, Hollis, Juneau, Ketchikan.
Host: *Tsuga heterophylla*
*Scierus annectens* LeC.
Distribution: Bonanza Cr. (nr. Fairbanks), Bullfrog Is., Fairbanks, John R., Kasilof, Sumit L. (Kenai Penin.), Klehini R., (N of Haines), Willow.
Host: *Picea glauca*
*Scierus pubescens* Sw.
Distribution: Bonanza Cr. (nr. Fairbanks), Summit L. and Swanson R. road (Kenai Penin.).
Host: *Picea glauca*
*Xylechinus montanus* Blackm.
Distribution: Bonanza Cr. (nr. Fairbanks), Swanson River road, Summit L. (Kenai Penin.).
Host: *Picea glauca.*

## Scolytinae

*Cryphalus pubescens* Hopk.
Distribution: Iliamna L.
Host: *Picea glauca.*
Remarks: New state record.
*Cryphalus ruficollis* Hopk.
Distribution: Bonanza Cr. (nr. Fairbanks), Charley R., John R., Summit L. (Kenai Penin.).Host: *Picea glauca.*
*Crypturgus borealis* Sw.
Distribution: Bonanza Cr. (nr. Fairbanks), Charley R., Coleen R., Echo Cove (nr. Juneau), Fairbanks, John R.
Hosts: *Picea glauca, P. sitchensis.*
*Dolurgus pumilus* (Mann.)
Distribution: Chichagof Is., Echo Cove and Gold Cr. (nr. Juneau), Hollis, Juneau, Montana Cr. (SE AK), Naukati Bay, Sitka Island, Yakutat.
Hosts: *Picea sitchensis, Tsuga heterophylla.*
*Dryocoetes affaber* (Mann.)
Distribution: Arviriaq (nr. Noatak R.), Bonanza Cr., Coleen R., Cooper Landing, Douglas, Dry Gulch (Kenai Penin.), Echo Cove (nr. Juneau), Fairbanks, Ft. Yukon, Hollis, Homer, John R, Juneau, Kandik R., Kasilof, Kenai National Moose Range, McKinley N.P., Mentasta, Mile 24, Mile 50, Montana Cr. (Mat-Su Valley), Moose Pass, Naukati Bay, Noatak R., Northway Junction, Patterson, Russian R., Sheenjek R., Summit L. (Kenai Penin.), Talkeetna, Venetie, Walker L., Yakutat.
Hosts: *Picea glauca, P.* x *lutzii, P. sitchensis, Pinus contorta.*
*Dryocoetes autographus* (Ratz.)
Distribution: Anchorage, Bonanza Ck. (nr. Fairbanks), Chandalar, Cooper Landing and Dry Gulch (Kenai Penin.), Edna Bay, Glacier Bay, Hollis, John R., Kandik R., Kenai National Moose Range, Ketchikan, M.34 Seward Hwy, Naukati Bay, Northway Junction, Patterson, Russian R., Summit L. and Sunrise (Kenai Penin.), Yakutat.
Hosts: *Picea glauca, P. sitchensis, Tsuga heterophylla.*
*Dryocoetes caryi* Hopk.

Distribution: Homer, Mile 34 Seward Hwy, Moose Pass and Russian R (Kenai Penin.).
Host: *Picea* x *lutzii*.

*Ips borealis borealis* Sw.
Distribution: Bonanza Cr. (nr. Fairbanks), Cooper Landing and Dry Gulch (Kenai Penin.), John R., Kenai National Moose Range, Nanana Hwy., Summit L.(Kenai Penin.), Wasky (nr. Togiak L.).
Hosts: *Picea glauca, P.* x *lutzii.*

*Ips concinnus* (Mann.)
Distribution: Echo Cove (nr. Juneau), Edna Bay, Hollis, Homer, Hoonah, Juneau, Kodiak Is., Mile 20, Montana Cr. (nr. Juneau), Rogers Point, Seagull Creek, Granite Cr. (Kenai Penin.), Seward.
Host: *Picea sitchensis, P. x lutzii.*

*Ips perturbatus* (Eichh.)
Distribution: Arctic Village, Arviriaq (nr. Noatak R.), Bonanza Cr. (nr. Fairbanks), Chandalar, Circle City, Coleen R., Cooper Landing and Dry Gulch (Kenai Penin.), Fairbanks, Ft.Yukon, Hope, Hughes, John R., Kandik R., Kasilof, Kenai National Moose Range, Klutina L., Lawing (Kenai Penin.), Mentasta, McKinley River drainage (24 mi E of Lake Minchumina), Mile 50, Northway Jct., Noatak R., Pah R., Porcupine R., Richardson Highway, Russian R. (Kenai Penin.), Sheenjek R. Summit L. (Kenai Penin.), Venetie, Walker L.
Host: *Picea glauca*, *P. x lutzii.*

*Ips pini* (Say)
Distribution: Douglas Is., Ketchikan, Petersberg.
Host: *Pinus contorta.*

*Ips tridens* (Mann.)
Distribution: Bonanza Cr. (nr. Fairbanks), Cooper Landing and Dry Gulch (Kenai Penin.), Echo Cr. (nr. Juneau), Richardson Highway, Rodgers Point (Chichagof Is.), Seward, Cove (nr. Juneau), Fick Cove (Chichagof Is.), Hollis, Homer, Hood Bay, John R., Juneau, McKinley N.P., Mile 34 Seward Hwy., Montana Cr. (Mat-Su Valley), Moose Pass and Quartz Cr. (Kenai Penin.), Sheenjek R., Sitka Is., Summit L. and Sunrise (Kenai Penin.), Willow.
Hosts: *Picea glauca*, *P.* x *lutzii*, *P. sitchensis*.
Remark: Two subspecies, *I. tridens tridens* (Mann.) and *I. tridens engelmanni* Sw., occur in Alaska (Wood 1982); however, the distributions given therein appear to overlap and further collecting is needed to clarify this point. According to Wood (1982), females of the latter subspecies tend to have a more protuberant and generally more pubescent frons.

*Lymantor alaskanus* Wood
Distribution: Bonanza Creek, 42 km W of Fairbanks.
Hosts: Unknown
Remark: This species was described (Wood 1982) from 19 specimens collected 18-VII-1978 on a sticky trap baited with Ipsenol (pheromone of *Ips* spp.) and *alpha*-pinene (resin constituent). Its host is unknown. The other North American species, *L. decipiens* LeC., infests dead, dry, branches of living maple trees. Its gallery penetrates the sapwood and is associated with black stain (Wood 1982).

*Orthotomicus caelatus* (Eichh.)

Distribution: Bonanza Creek (nr. Fairbanks), Circle City, Douglas, John R., Juneau, Kandik R., McKinley River drainage (24 mi E of Lake Minchumina), Mile 7, Petersburg, Porcupine R.

Hosts: *Picea glauca, P. sitchensis, Pinus contorta.*

*Pityophthorus bassetti* Blkm.

Distribution: Bonanza Cr. (nr. Fairbanks), Fairbanks.

Host: *Picea glauca.*

*Pityophthorus murrayanae murrayanae* Blackm.

Distribution: Bonanza Cr. (nr. Fairbanks), Hope, Mile 295 Richardson Hwy., Sheenjek R., Summit L. (Kenai Penin.).

Hosts: *Picea glauca, P.* x *lutzii.*

*Pityophthorus nitidulus* (Mann.)

Distribution: Anchorage, Bonanza Cr. (nr. Fairbanks), Cooper Landing and Dry Gulch (Kenai Penin.), Eagle R., Hollis, Homer, Iliamna L., Juneau, Kenai National Moose Range, Kodiak Is., Lawing, Moose Pass, Quartz Cr. (Kenai Penin.), Seward, Skilak L., Summit L. (Kenai Penin.).

Hosts: *Picea glauca, P.* x *lutzii, P. mariana, P. sitchensis.*

*Pityophthorus nitidus* Sw.

Distribution: Bonanza Cr. (nr. Fairbanks), Fort Yukon, Hope, John R., Lawing (Kenai Penin.), Summit L. (Kenai Penin.).

Hosts: *Picea glauca, P.* x *lutzii.*

*Pityophthorus opaculus* LeC.

Distribution: Bonanza Creek (nr. Fairbanks), Fairbanks, Hope, John R., Summit L. (Kenai Penin.).

Hosts: *Picea glauca, P.* x *lutzii.*

*Pityophthorus recens* Bright

Distribution: Granite Cr. (Kenai Penin.).

Host: *Picea* x lutzii.

Remark: New state record. Hundreds of specimens were captured in funnel traps during field tests of *Ips perturbatus* pheromones.

*Pityophthorus tuberculatus* Eichh.

Distribution: Haines, Juneau, Skagway (Bright 1981).

Host: *Pinus contorta.*

*Procryphalus mucronatus* (LeConte)

Distribution: Hope.

Host: Unknown.

*Procryphalus utahensis* (Hopk.)

Distribution: Bonanza Creek (nr. Fairbanks), Galena.

Hosts: *Salix scouleriana, Salix* sp.

*Pseudips* (=*Ips*) *mexicanus* (Hopk.)

Distribution: Douglas Is., Juneau.

Host: *Pinus contorta.*

Remark: Cognato (2000) transferred *Ips mexicanus* to the new genus *Pseudips.*

*Scolytus piceae* (Sw.)

Distribution: Bonanza Cr. (nr. Fairbanks), Fairbanks, Ft.Yukon, John R., Northway Junction, Walker L.

Hosts: *Picea glauca, Larix laricina.*

*Trypodendron betulae* Sw.

Distribution: Anchorage, Chichagof Is., Fairbanks.

Host: *Alnus sinuata, Betula papyrifera.*

Remarks: New state record.

*Trypodendron lineatum* (Oliv.)

Distribution: Admiralty Is., Auke Bay, Bonanza Cr. (nr. Fairbanks), Chichagof Is., Cooper Landing, Cordova, Dry Gulch (Kenai Penin.), Edna Bay, Fairbanks, Hollis, Homer, John R., Kenai National Moose Range, Petersburg, Russian R. and Summit L. (Kenai Penin.), White Bay, Yakutat.

Hosts: *Picea glauca, P. sitchensis, Pinus contorta, Tsuga heterophylla.*

*Trypodendron retusum* (LeC.)

Distribution: Anchorage, Bonanza Cr. (nr. Fairbanks), Russian R., Summit L. and Sunrise (Kenai Penin.), Willow.

Hosts: *Betula papyrifera, Populus tremuloides.*

*Trypodendron rufitarsus* (Kby.)

Distribution: Russian R. (Kenai Penin.), Talkeetna, Sunrise (Kenai Penin.).

Hosts: *Picea glauca, Tsuga mertensiana.*

*Trypophloeus striatulus* (Mann.)

Distribution: Interior, coastal NW, N Slope; wherever its host occurs.

Host: *Salix alaxensis.*

Remarks: Collected at Shublik Spring, Canning River, Lat. N 69° 30', possibly the farthest north of any scolytid. A fungus, *Cytospora* sp. is universally present in infested stems indicating a possible symbiotic relationship. The same stem is infested by several generations of the beetle before killing it (Furniss 1997).

## ACKNOWLEDGEMENTS

We thank Kenneth P. Zogas, USDA Forest Service, Forest Health Protection, Anchorage, Alaska for curating the Alaska insect collection for the last twenty years and for compiling the list of accessions used herein. The manuscript was reviewed by Donald E Bright, Jr. and Stephen L. Wood who also identified most of the bark beetles recorded here. Other reviewers who contributed to improvement of the paper were Roger E. Burnside and Richard A.Werner.

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# Searching behaviour of *Trichogramma* wasps (Hymenoptera: Trichogrammatidae) on tomato and pepper leaves

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## ABSTRACT

Walking speeds of both *Trichogramma brassicae* and *T. sibericum* were substantially lower on tomato than on pepper leaf disks. The difference may be due to the presence of glandular trichomes on tomato foliage. Total time spent on leaf disks during behavioural trials was lower on tomato than on pepper leaf disks for both species of wasps. This may indicate a higher propensity to disperse from tomato foliage than from pepper foliage. Lower walking speeds and shorter residence times on tomato leaves could result in a lower searching efficiency of wasps on tomato than on pepper. The subsequent efficacy of *Trichogramma* for biological control of cabbage loopers in greenhouses may be lower on tomato crops than on pepper crops.

**Key words:** *Trichogramma brassicae*, *Trichogramma sibericum*, *Trichoplusia ni*, searching behaviour, glandular trichomes, egg parasitoids, biological control, greenhouse vegetables

## INTRODUCTION

Foliar pubescence on agricultural crops may interfere with the host location activities of small entomophagous insects and mites and reduce their subsequent effectiveness for biological control of arthropod pests (Obrycki 1986). Such effects have been documented for a variety of taxa. The predatory mite, *Phytoseiulus persimilis* Athias-Henriot (Acarina: Phytoseidae), was trapped by glandular trichomes more frequently on a tomato variety with a high trichome density than on a relatively hairless tomato variety (van Haren *et al.* 1987). Walking speed and parasitism of greenhouse whitefly (*Trialeurodes vaporariorum* (Westwood) (Homoptera: Aleyrodidae)) by *Encarsia formosa* Gahan (Hymenoptera: Aphelinidae) was lower on cucumber varieties with higher levels of foliar pubescence (van Lenteren *et al.* 1995). Walking speeds of *E. formosa* recorded on pubescent tomato and gerbera foliage were slower than those recorded on hairless sweet pepper (Sutterlin & van Lenteren 1997). The estimated searching efficiency of *Orius insidiosus* (Say) (Heteroptera: Anthocoridae) was lowest on pubescent tomato foliage compared to corn and bean foliage (Coll *et al.* 1997). Higher prey handling times were recorded for *Podisus nigrispinus* (Dallas) (Heteroptera: Pentatomidae) on tomato plants compared to those recorded on eggplant or pepper plants (De Clerq *et al.* 2000). In this study, we compare the searching behaviour of *Trichogramma brassicae* Bezdenko and *T. sibericum* Sorokina (Hymenoptera: Trichogrammatidae) on tomato and pepper leaf disks in the laboratory.

Wasps of the genus *Trichogramma* are egg parasitoids that have been used widely for biological control of Lepidopteran pests (Li 1994). Searching behaviour and parasitism of hosts by a number of *Trichogramma* species are impeded by high levels of foliar pubescence. The time required to walk across leaf disks, the percentage of wasps initiating flight before crossing leaf disks, and the number trapped by trichomes were all higher for *T. pretiosum* Riley on tomato varieties with higher densities of glandular trichomes and containing either 2-tridecanone or 2-undecanone (Kashyap *et al.* 1991). In a field study, the highest levels of parasitism of *Heliothis* spp. eggs (Lepidoptera: Noctuidae) by *T. pretiosum* and *T. exiguum* Pinto & Platner were observed on tomato varieties with the lowest density of glandular trichomes (Kauffman & Kennedy 1989). Walking speeds of *T. exiguum* were lowest on highly-pubescent mullein, intermediate on intermediately-pubescent tomato, and highest on relatively hairless maize and soybean (Keller 1987). Parasitism of *Heliocoverpa armigera* (Hübner) (Lepidoptera: Noctuidae) eggs by *T. chilonis* Ishii on pigeonpea varies widely across plant parts depending on the presence of trichomes. Parasitism is much lower on pods and calyxes that have a higher trichome density than on leaves (Romeis *et al.* 1998; 1999).

*T. brassicae* are released in British Columbia vegetable greenhouses for biological control of cabbage loopers (*Trichoplusia ni* (Huebner) (Lepidoptera: Noctuidae)) (Portree 1993). *T. sibericum* has been evaluated for management of cabbage loopers in vegetable greenhouses (E.S. Cropconsult Ltd., unpublished report). Although *Trichogramma* wasps are released in both tomato and pepper crops, no previous comparisons of searching behaviour on tomato and pepper foliage have been done. Previous work has shown that yellow sticky traps (that are used to monitor dispersal by *T. brassicae*) capture fewer wasps in tomato greenhouses than in pepper greenhouses (E.S. Cropconsult Ltd., unpublished data). In addition, numerous dead wasps have been found near release sites on tomato stems, presumably trapped by glandular trichomes (Prasad, personal observation). Both of these observations indicate that *Trichogramma* wasps may be less efficient for biological control of cabbage loopers on tomato than on pepper crops.

For the purposes of this paper, searching behaviour in *Trichogramma* is considered to be all activities that facilitate the location of suitable host eggs including walking on and examining host-free leaf surfaces. Here, we report measurements of walking speed on, time elapsed before exiting from, and proportion of time spent searching on excised tomato and pepper leaf disks in the laboratory by *T. brassicae* and *T. sibericum* females. Our objective was to identify differences in the behaviour of wasps between these two plant species caused by the presence of glandular trichomes on tomato leaves.

## MATERIALS AND METHODS

*Insects. Trichogramma sibericum* were reared on sterilized *Ephestia kuehniella* eggs. *T. sibericum* females used in bioassays were between 1 and 3 d old. *T. brassicae* were obtained from Beneficial Insectary (Oak Run, California) and were 3 to 5 d old when used in trials. All wasps were provided continuously with dilute honey (50% by volume) applied as droplets to the inner surface of holding containers.

*Bioassay arenas.*Tomato and pepper leaves of unknown variety were collected from commercial greenhouses, wrapped in damp paper towelling, stored in Zip-lock® bags at 5° C, and used in trials within 5 d of collection. Arenas for measurement of searching behaviour consisted of leaf disks (2 cm in diameter) cut with a cork borer from tomato or pepper leaves and attached (underside up) to the bottom half of 9 cm plastic petri-dishes using double-sided tape. Behavioural observation and video recording were facilitated by confining wasps to this simple two-dimensional arena in the absence of host eggs. *Trichogramma* females search for hosts on both upper and lower leaf surfaces on entire plants (McGregor, personal observation). Here, we assume that the behaviour wasps display in this simple bioassay is analogous to behaviour displayed on whole plants in the field. The underside of leaves was used for trials because it has a higher density of trichomes on tomato leaves than the upper surface. Ten arenas (five tomato and five pepper) were prepared at a time for use in bioassays. After ten trials were completed, ten more arenas were prepared. This prevented leaf disks from deteriorating before use in bioassays.

*General bioassay procedure.* For each trial, a female wasp was released in the center of a tomato or pepper leaf disk from the tip of a fine paintbrush. The wasp was videotaped using a Panasonic WV-CD110 camera fitted with a Tamron 72mm camera lens and run by a Panasonic WV-PS10 drive unit., The position of the camera and zoom lens were adjusted until the two-cm leaf disk filled most of the screen on a video monitor. Wasps were videotaped for 5 min or until they flew or walked off the leaf disk. All trials were run under ambient conditions in the laboratory (temperature: 21-25° C; relative humidity: 37-65%). The trial area was illuminated from above with a single incandescent bulb (60 watt). Trials were alternated between plant species. Twenty trials were completed for each wasp species on each plant species (ie. total of 80 trials).

*T. sibericum bioassays.* All *T. sibericum* bioassays were run as above. However, trials that lasted less than 60 s were discarded. This was done to maximize the number of walking tracks that could be analysed for each wasp in order to increase the precision of estimates of walking speed. The first 20 trials for each plant species that lasted more than 60 seconds were retained for analysis.

*T. brassicae* bioassays. The majority of trials for this species lasted less than 60 seconds so none was discarded. The wasps walked or flew off the leaf shortly after release in most cases. The first 20 trials for each plant species were retained for further analysis no matter how short in duration.

*Estimation of walking speed.* An acetate sheet was taped to the screen of the video monitor. Walking tracks of *Trichogramma* females were traced with a felt pen on the acetate sheet. Tracks were only traced and analysed for walking on the surface of the leaf disk. Walking along the edge of the leaf disk was not recorded. One to five tracks of at least 1 cm were traced for each wasp. Tracing of a particular track was stopped when the wasp reached the edge of the leaf disk. The time a wasp spent walking along a traced path was recorded with a stopwatch. The length of the path was measured on the acetate sheet using a cartographer's odometer. The odometer consists of a rotating wheel (and associated accumulating scale) that is rolled along a curved line to measure its length in odometer units. Odometer units were calibrated to the image from the video display by measuring a tracing of a video clip of a centimeter ruler filmed at the same position that bioassays were conducted. Walking speed for each wasp was calculated by dividing the sum of the distance travelled in all measured tracks by the sum of the times recorded for walking those tracks.

*Measurement of searching time and residence time.* The videotape of each trial was viewed from the time of release of the wasp until the end of the trial. The total time each wasp spent on the leaf disk during the trial ("residence time") was recorded using a stopwatch (ie. the time from release until the time the wasp walked or flew off the leaf or until the trial was stopped at 5 m). As such, residence time ranged from zero to 300 s. Searching time was recorded on a second stopwatch as the time the wasp spent walking on the leaf disk during the trial. Time spent resting and cleaning wings or antennae was not included. The proportion of time spent searching during a trial was calculated by dividing searching time by residence time.

*Data analysis.* Data for all trials for both *Trichogramma* species and both leaf species were combined for analysis. The variables walking speed, total time spent on the leaf disk and proportion of time spent searching during the trial were analysed by two-factor analysis of variance (ANOVA) where the factors were *Trichogramma* species (WASP) and leaf species (LEAF). Data for proportion of time spent searching were arcsin-square root-transformed before analysis to normalize data. Untransformed means are reported for proportion of time spent searching. All analyses were conducted using Sigmastat version 2.0 (Fox *et al.*, 1995).

## RESULTS

*Walking speed.* Walking speed was significantly higher (approximately twice as fast) on pepper leaves than on tomato leaves for both *Trichogramma* species (Table 1, Table 2). There was no significant difference in walking speed between the two *Trichogramma* species. There was also no difference in how variation in walking speed in the two wasp species was affected by the two plant species as indicated by the non-significant interaction term in the ANOVA.

**Table 1**

Mean walking speed, residence time and proportion of time spent searching (Mean ± SE) by female *Trichogramma* wasps on tomato and pepper leaf disks.

| Variable | *T. sibericum* | | *T. brassicae* | |
|---|---|---|---|---|
| | Tomato | Pepper | Tomato | Pepper |
| Walking speed (mm/sec) | 0.9 ± 0.1 | 2.0 ± 0.2 | 1.1 ± 0.1 | 2.3 ± 0.2 |
| Residence time (seconds) | 219 ± 21 | 248 ± 19 | 48 ± 8 | 89 ± 20 |
| Proportion of time spent searching | 0.68 ± 0.05 | 0.63 ± 0.03 | 0.82 ± 0.06 | 0.73 ± 0.05 |

**Table 2**

Two-factor analysis of variance of walking speed, residence time and proportion of time spent searching by female *Trichogramma* wasps. Factors for analysis are wasp species (WASP; either *T. sibericum* or *T. brassicae*) and plant species (PLANT; either tomato or pepper leaf disks).

| Variable | Factor | F | df | p |
|---|---|---|---|---|
| Walking speed | WASP | 2.1 | 1 | 0.15 |
| | LEAF | 64.5 | 1 | <0.001 |
| | WASP*LEAF | 0.3 | 1 | 0.62 |
| Residence time | WASP | 89.0 | 1 | <0.001 |
| | LEAF | 4.0 | 1 | 0.048 |
| | WASP*LEAF | 0.1 | 1 | 0.73 |
| Proportion of time spent searching | WASP | 10.1 | 1 | 0.002 |
| | LEAF | 3.3 | 1 | 0.07 |
| | WASP*LEAF | 0.5 | 1 | 0.49 |

*Residence time on leaf disk.* Both *Trichogramma* species and leaf species affected the residence time of wasps on leaves (Table 1, Table 2). *T. brassicae* females spent significantly less time than *T. sibericum* on both tomato and pepper leaf disks. However, this reflects the manner in which trials were conducted for the two *Trichogramma* species. *T. sibericum* trials of less than 60 s were rejected and this artificially inflated the mean residence times for this species. Because *T. brassicae* females dispersed from leaf disks more readily than *T. sibericum* females, shorter trials were retained for analysis. For both wasp species, LEAF was a significant effect (ie. more time was spent on pepper than on tomato leaf disks). Wasps exited earlier from tomato foliage than from pepper foliage in trials. Variation in residence time in both wasp species was affected similarly on the two plant species as indicated by the non-significant interaction term in the ANOVA.

*Proportion of time spent searching.* Leaf species did not significantly affect the proportion of time that females spent searching while on leaf disks during trials (Table 1, Table 2). However, the proportion of time that females spent searching on leaf disks was significantly higher for *T. brassicae* than for *T. sibericum*. Again, this reflects the difference in the manner in which trials were conducted for the two species. *T. brassicae* trials often consisted of the wasp walking to the leaf edge and directly off the edge after release. This sort of trial has a proportion of time spent searching of 1 (or 100% of time searching), and was much more common for *T. brassicae* than for *T. sibericum*. Again, the interaction term was non-significant indicating that both wasp species react in a similar fashion to the two leaf species.

## DISCUSSION

There are clear effects of leaf species on the behaviour of both *T. brassicae* and *T. sibericum*. First, wasps walk at approximately half the speed on tomato leaf disks as on pepper leaf disks. This difference was consistent in two *Trichogramma* species of different ages and physiological conditions. Such a reduction of walking speed on tomato is similar to what has been reported for other *Trichogramma* species and is probably caused by the presence of glandular trichomes which impair the walking behaviour of wasps (Keller 1987; Kauffman & Kennedy 1989; Kashyap *et al.* 1991). Second, wasps leave tomato foliage (with trichomes) sooner than they leave pepper foliage (without trichomes). This result may indicate a lower preference for tomato foliage than pepper foliage as a habitat for host search. A higher propensity to disperse from foliage with higher trichome densities has previously been reported for *T. pretiosum* (Kashyap *et al.* 1991). Because the wasps walked faster and stayed longer on pepper leaf disks, they likely examined more of the leaf surface available than wasps on tomato leaf disks.

The *T. brassicae* females used in this study were more behaviourally active and dispersed from leaf disks much more readily than *T. sibericum* females. This behavioural difference could be genetically based, caused by the difference in age between the groups of wasps (*T. brassicae* were 3-5 d old; *T. sibericum* were 1-3 d old), or caused by some other difference in physiological condition that influences dispersal. Whatever the explanation, the consistency of walking speed measurements for these two behaviourally-distinct groups of insects is remarkable. Also, despite differences in residence time between *T. brassicae* and *T. sibericum* caused by different bioassay methods, we still detected lower residence times on tomato leaf disks than on pepper for both species.

We have assumed that our measurements of behaviour on a two-dimensional excised leaf disk are analagous to behaviour on whole plants under field conditions. In addition, we have assumed that wasps are searching for hosts or evaluating leaf surfaces as host habitat when walking on leaf surfaces in the laboratory. Our method allowed the detection of behavioural differences between two plant species that are likely caused by the presence of trichomes on tomato. Measurement of walking speed in the laboratory has been recommended to evaluate performance quality for mass-reared *Trichogramma* wasps (Cerutti & Bigler 1994), although this measure of quality does not always correlate with parasitism success (van Hezewijk *et al.* 2000). In light of the results presented here, it seems critical to measure walking speed on the appropriate plant substrate. Prediction of performance on tomato crops using walking speed data from pepper leaves would overestimate searching efficiency of both species of wasps.

Our results show that both *T. brassicae* and *T. sibericum* behave differently on tomato leaf disks than on pepper leaf disks. If these behavioural differences also occur during searching behaviour in commercial greenhouses, the resulting level of biological control could be lower in tomato greenhouses vs. pepper greenhouses. Wasps might discover fewer hosts on tomato because lower walking speed and a higher tendency to exit tomato foliage would reduce the number of hosts encountered per unit time. This hypothesis has important implications for release rates of *Trichogramma* in the two crops (ie. higher release rates may be required in tomato greenhouses). However, our laboratory-derived results should be validated by conducting releases of *Trichogramma* into tomato and pepper crops under operational conditions.

## ACKNOWLEDGEMENTS

We thank the British Columbia Greenhouse Research Council for financial assistance. Many thanks to Bernie Roitberg for the use of his laboratory and video equipment for the purposes of the study.

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# *Stylops shannoni* (Stylopidae, Strepsiptera): A New species for Canada, with comments on *Xenos peckii*

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## ABSTRACT

The collection of a male *Stylops shannoni* Pierce and a number of stylopized bees, *Andrena hippotes* Robertson, containing both male and female strepsipterans is reported. This appears to be the first host record and the first association of males and females for this strepsipteran species. This also appears to be the first record for *S. shannoni* in Canada. In addition, a specimen of *Polistes fuscatus* stylopized by *Xenos peckii* Kirby was found in the collection of the Spencer Entomological Museum at the University of British Columbia.

## INTRODUCTION

Strepsiptera is an order of peculiar parasitic insects. Taxonomically, strepsipterans have had an unsettled history, having been included in at least five different orders with a rank ranging from subfamily to full ordinal status (Bohart 1941). Strepsipterans are now usually placed in their own order, closely allied with Coleoptera (Kukalová-Peck & Lawrence 1993).

Strepsipterans are not often observed. The females of most species are neotenic and remain permanently in the host; the adult males, though free-flying, are small and short-lived. I report the collection of an adult male strepsipteran and a number of stylopized bees. In addition, I report on a stylopized specimen of paper wasp found in the Spencer Entomological Museum collection (SEMC) at the University of British Columbia.

## MATERIALS AND METHODS

In early April, 2000, during an informal biodiversity survey of my yard in Richmond, British Columbia, I collected a free-flying male strepsipteran. In the same area was a flowering bush which was being visited by a number of species of Hymenoptera and Diptera. Among the Hymenoptera were bees belonging to the families Apidae, Halictidae and Andrenidae, the last being *Andrena* sp., some of which were stylopized (Fig. 1). Over the next three weeks, I monitored the bees visiting the bush. Because the neighborhood is residential, I was unable to follow the bees leaving the bush to determine the location of their nests. One bee was found under a clod of earth near the base of the bush but I could find no evidence of a nest in that area. Three of the female strepsipterans were dissected from their hosts and fixed in gluteraldehyde for electron microscopic examination. The puparium of one of the males was opened and the male removed. Several stylopized bees were coated with gold-palladium and photographed using a scanning electron microscope at 20 kV.

## RESULTS

Between 9–18 April 2000, I collected 88 *Andrena* sp. in my front yard, of which 24 were parasitized. During the warmest part of the day, 1200–1400 hours, the stylopization rate of these *Andrena* sp. was about one in three. This rate dropped to about one in ten for collections before 10:00. No more free-flying males were observed after the initial collection but several bees contained open puparia, indicating males had emerged, and three males still in their puparia were collected. The latter three specimens were in multiply stylopized bees, one with a female and the other two each with a second male which had emerged prior to collection of the bee (Fig. 1c).

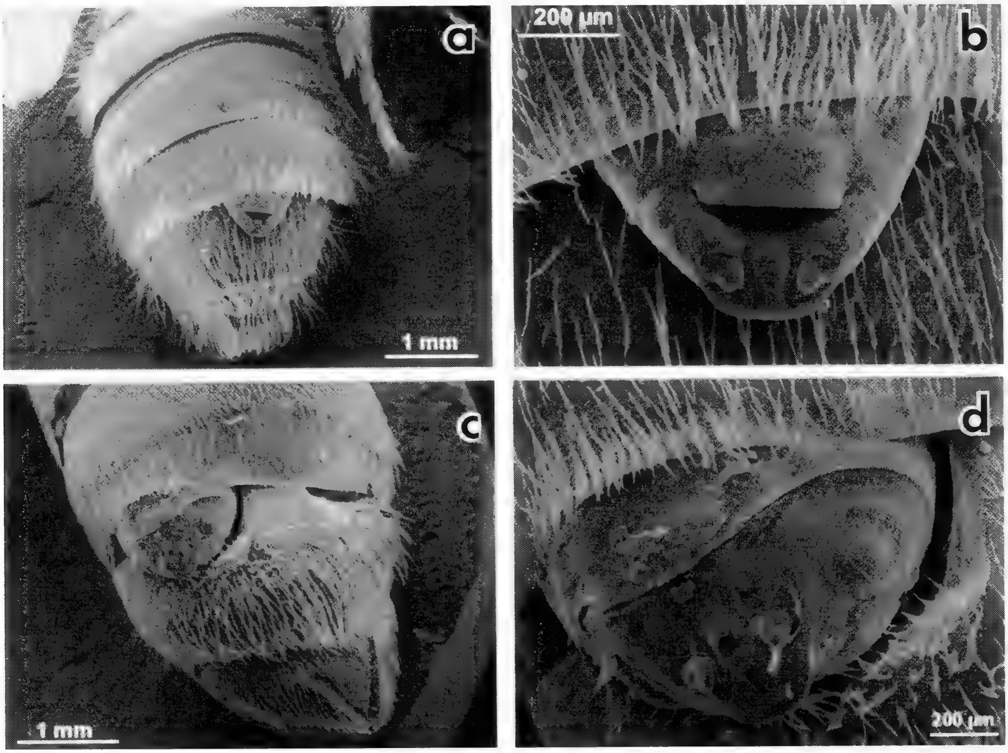

**Figure 1**. Scanning electron micrographs of *Andrena (Trachandrena) hippotes* Robertson stylopized by *Stylops shannoni* Pierce. **a** and **b**: female *S. shannoni*; **c**: male *S. shannoni* in its puparium (left) with an open puparium (right) from which a second male had emerged prior to collection of the bee; **d**: close up of male puparium.

Using standard keys (Borrer *et al.* 1989), I was able to confirm that the male strepsipterans were *Stylops* sp. as expected from the fact that they were parasitizing *Andrena* sp. Two mature males and the fixed female specimens were submitted to J. Kathirithamby who determined the males to be *Stylops shannoni* Pierce. W. E. LaBerge and R. Brooks determined the host bees to be *Andrena (Trachandrena) hippotes* Robertson. Voucher specimens of both the strepsipterans and the host bees have been deposited in the SEMC.

While collating data with respect to paper wasps in the SEMC, a stylopized specimen with a locality label of Vancouver was found. It carried a female strepsipteran with its head extruded between tergites three and four.

## DISCUSSION

*Stylops shannoni* was known previously only from a free-flying male collected on Plummer's Island, Maryland (Pierce 1918, Bohart 1941). As far as I have been able to determine, this is the first time males and females of *S. shannoni* have been collected together and this is the first host record for this enigmatic species. Although the host species for *S. shannoni* in Maryland was not determined, *A. hippotes* is found there (LaBerge 1973). If *S. shannoni* is generally associated with *A. hippotes*, it could be found in much of North America since *A. hippotes* has a transcontinental range extending from southern British Columbia to central California on the west coast and Nova Scotia to Georgia on the east coast (LaBerge 1973).

*Stylops erigeniae* Pierce is known only from a female also collected on Plummer's Island (Pierce 1918). Bohart (1941) suggested that "it is probable that *shannoni* represents the male of *erigeniae*". Pierce, who was under the mistaken impression that *Stylops* spp. are strictly monospecific with respect to host species, erected a new species, *S. hippotes* Pierce, for a female stylopizing *A. hippotes* which was collected in Ohio (Pierce 1909). Bohart (1941) in his revision of North American Strepsiptera lists *S. hippotes* as a species of "uncertain position". Perhaps *S. shannoni* is the male of *S. hippotes*.

Due to the lack of distinctive morphological characters, female *Stylops* spp. are difficult to identify (Kathirithamby 1989). Added to that, the poor condition of many of Pierce's type specimens (Bohart 1941) will make resolution of these possible synonymies very difficult. Kathirithamby (personal communication) suggests that DNA analysis will be required to match males and females.

The stylopized paper wasp found in the SEMC is *Polistes fuscatus* (Fabricius). It is not *P. f. aurifer* Saussure, the subspecies which commonly occurs in BC as it has no yellow spots on tergite two. It is darker overall than typical *P. f. aurifer* even taking into account the variant formerly called *P. f. montanus* Bequaert (Bequaert 1940). The wasp keys out to *P. f. fuscatus* (Bequaert 1940, 1942). Although some records of *P. f. fuscatus* in BC have been attributed to "assisted transport" (Buckell & Spencer 1950), Leech (1966) reports the collection near Vernon in 1947 of a stylopized paper wasp which was determined as *P. f. variatus* Cresson. *Polistes f. variatus* has subsequently been synonymized with *P. f. fuscatus* (Snelling 1974). It seems unlikely that Leech's record is the result of "assisted transport".

The wasp Leech collected had two puparia projecting between tergites five and six, one laterally and one ventrally. Leech extracted the two male strepsiperans and they were determined as *Xenos peckii* Kirby (Leech 1966). One of these specimens was submitted to the SEMC in 1958 although its current location is not known. The female strepsipteran in the SEMC *P. fuscatus* specimen also appears to be *X. peckii*. The positions of the strepsipterans in both cases appear to be unusual. According to Salt & Bequaert (1929), in *Polistes* sp., male strepsiptera are usually located under tergites 3 or 4 while females are usually under tergite 5. Further, all examples cited by those authors of extrusion on the ventral surface of the wasp involve wasps with three or more parasites.

Based on the records presented here, both *Stylops shannoni* and *Xenos peckii* should be added to the Canadian and BC species lists given in Peck (1991).

## ACKNOWLEDGEMENTS

I thank J. Kathirithamby for helpful comments and for determining the strepsipterans, W. E. LaBerge and R. Brooks for determining the host bees, A. Behennah for finding the stylopized *Polistes* sp., E. Humphrey for use of supplies and facilities of the BioSciences Imaging Centre, G. S. Kenner for taking the micrographs in Figure 1.

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# Short-range horizontal disruption by verbenone in attraction of mountain pine beetle (Coleoptera: Scolytidae) to pheromone-baited funnel traps in stands of lodgepole pine

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## ABSTRACT

Verbenone interrupted the attraction of mountain pine beetle, *Dendroctonus ponderosae* Hopkins, to baited multiple-funnel traps at a distance of <4 m. Catches of beetles in traps placed ≥4 m from traps with verbenone were not significantly lower than catches in control traps. These results are consistent with the short-range phenomenon of "switching" exhibited by mountain pine beetle in the formation of a spot infestation in stands of lodgepole pine.

**Key words:** *Dendroctonus ponderosae,* Coleoptera, Scolytidae, verbenone, antiaggregation pheromone, multiple funnel trap

## DISCUSSION

Non-destructive semiochemical-based tactics to control populations of the mountain pine beetle, *Dendroctonus ponderosae* Hopkins, are appealing where resource management objectives cannot tolerate removal of infested trees (Borden and Lindgren 1988). Verbenone is an antiaggregation pheromone used by *D. ponderosae*, to interrupt attraction of beetles to trees already colonized by beetles (Lindgren and Borden 1989). However, operational trials of verbenone to disrupt populations of mountain pine beetles have had mixed success in stands of lodgepole pine, *Pinus contorta* var. *latifolia* Engelmann, (Amman and Lindgren 1995). Verbenone has been ineffectual in stands of ponderosa pine, *P. ponderosae* Laws. (Bentz et al. 1989). Two methods of application have been used in these verbenone trials: (1) aerially-applied verbenone-impregnated polyethylene beads; or, the most common method, (2) bubblecaps containing verbenone and attached to trees in a grid system. The concentration of bubblecap devices deployed in most trials in British Columbia has been about 100/ha (10 by 10 m spacing regime) (Amman and Lindgren 1995). My objective was to assess the effective range of verbenone, released from bubblecaps, in interrupting the attraction of *D. ponderosae* to its aggregation semiochemicals over a range of 10 m.

On 17 August 1991, seventy 12-unit Lindgren multiple-funnel traps (Phero Tech Inc., Delta BC) were deployed in stands of mature lodgepole pine near Penticton, British Columbia, in ten sets of seven traps per set. The infestation levels of pines by *D. ponderosae* in these stands varied from 10-20% of live trees. One trap in each set was randomly positioned, serving as the first trap for the subsequent array of traps along a randomly selected compass direction. Five additional traps within each set were positioned in a linear array, starting 2 m from the first trap, with a space of about 2 m between traps. The seventh trap in each set was set 10 m from the last trap in the array (20 m from the first trap) and in the same line, to test if the effect of verbenone was similar across a distance of 10 m. Each trap was hung between trees with twine such that the bottom of each trap was about 0.5 m above ground. No trap was within 2 m of any tree. Sets of traps were spaced 1

– 5 km apart. All traps were baited with the primary aggregation semiochemicals for *D. ponderosae* (Skillen et al. 1997): (±)-*exo*-brevicomin flex lure (chemical purity >98%); polyethylene bubblecap lure containing a 13:87 mixture of *cis*-and *trans*-verbenol [chemical purities 98%, enantiomeric composition 83:17 (–):(+)]; and polyethylene bottle containing myrcene (chemical purity >95%). In five randomly selected sets of traps (designated as treated), the first trap in the array was baited additionally with a verbenone bubblecap (black polyethylene bubblecap containing verbenone [chemical purity >98%, enantiomeric composition 83:17 (–):(+)]). All lures were supplied by Phero Tech Inc. (Delta, British Columbia). The remaining five sets of traps were designated as controls. The verbenols were released at a combined rate of about 1.74 mg/d at 24 °C whereas verbenone and myrcene were released at about 14 and 281 mg/d at 24-28 °C, respectively (determined by weight loss) (PheroTech Inc. unpublished data). *exo*-Brevicomin was released at about 0.01 mg/d at 24 °C (determined by collection of volatiles) (PheroTech Inc. unpublished). Catches of insects were collected on 7 September 1991, terminating the experiment. Voucher specimens were deposited at the Entomology Museum, Pacific Forestry Centre (Victoria, British Columbia). The data were analyzed with the SYSTAT statistical package version 9.0 (SPSS 1998). Trap catch data [transformed by $\ln(y + 1)$] for control and treatment were subjected separately to one-way analysis of variance (ANOVA) using position of trap as the model factor. Fisher's least significant difference (LSD) multiple range test was performed when $P \leq 0.05$. Paired *t*-tests were used to compare mean catches in control and treatment traps for traps >4 m from the first trap.

**Table 1.**

Total catches of *Dendroctonus ponderosae* in baited Lindgren multiple-funnel traps from 20 August to 7 September 1991 near Princeton, British Columbia.

| | Mean (±SE) number of beetles [a] | |
|---|---|---|
| Distance of trap from 1st trap (m) | Control ($n = 5$) | Verbenone treatment ($n = 5$) |
| 0 | 92 ± 19.9 a | 9 ± 2.9 a |
| 2 | 86 ± 13.3 a | 46 ± 15.6 b |
| 4 | 78 ± 19.3 a | 70 ± 20.4 bc |
| 6 | 86 ± 17.6 a | 56 ± 10.7 bc |
| 8 | 86 ± 22.4 a | 97 ± 20.8 c |
| 10 | 59 ± 16.3 a | 81 ± 19.0 bc |
| 20 | 98 ± 21.2 a | 70 ± 19.7 bc |

[a] Means within the same column followed by the same letter are not significantly different at $P < 0.05$ (LSD test).

The effective range of verbenone in this study seemed to be less than 4 m from the release point (Table 1). There was a significant difference among mean trap catches of *D. ponderosae* in the treated set of funnel traps ($F_{6,28} = 6.733$, $P < 0.001$), with catches of beetles significantly lower in traps baited with verbenone than in any of the other traps in the treated set. There was no significant difference among mean trap catches of *D. ponderosae* in the control set of funnel traps ($F_{6,28} = 0.634$, $P = 0.702$) with a mean (±SE) catch of 84 ± 7 beetles per trap. The mean (±SE) total catch of *D. ponderosae* in traps ≥4 m in the control set (403 ± 83 beetles/set) was not significantly different from the mean total catch of beetles in traps ≥4 m from the verbenone-baited trap in the treated set (374 ± 69 beetles per set) ( *t* test, df = 8, $P = 0.795$). Results from this study suggest that using the existing type of bubblecap device to disrupt aggregations of *D. ponderosae* in stands of lodgepole pine would require deployment of devices at a much higher density, and subsequently would require an excessively high number of bubblecaps (>600-700 devices per ha at a spacing of 2–4 m). Further tests of verbenone to disrupt attacks by *D. ponderosae* should consider devices releasing verbenone at rates much higher than that of the black verbenone bubblecap used in past trials (about 14 mg/d at 24-28 °C).

## ACKNOWLEDGEMENTS

I thank B. Bentz, B.S. Lindgren and K.O. Britton for reviews of the manuscript. J.E. Brooks and D. Bartens provided field assistance. This study was supported by Forest Renewal British Columbia (FRBC).

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# Flight Tunnel and Field Evaluations of Sticky Traps for Monitoring Codling Moth (Lepidoptera: Tortricidae) in Sex Pheromone-treated Orchards

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## ABSTRACT

Delta, diamond, and wing style sticky traps baited with codlemone were evaluated in both flight tunnel and in field trials to determine their performance in capturing male codling moth *Cydia pomonella* (L.). Flight tunnel studies found no differences among trap types in terms of moth orientation behaviors. However, the proportion of moths contacting each trap type that were caught varied significantly. The 1CP wing trap caught a lower proportion of moths than the IIB diamond trap due to a significantly lower efficiency in retaining moths that landed on the trap. The position of a moth's first contact varied among traps with a significantly higher proportion landing on the outside of the wing style versus the delta and diamond traps. A significantly lower proportion of moths first landing on the outside of the delta trap were caught than for moths landing on the outside of the 1C wing trap. A significantly lower proportion of moths landing on the front opening of the 1CP wing trap were captured than for the other traps. No differences were found among trap types for either the proportion of moths flying into traps or the proportion of these moths captured. A majority of moths orienting to the diamond and delta traps first landed on the front flap and walked into the trap. The removal of the front flap from these traps did not affect their efficiency. However, a significantly greater proportion of moths flew directly into the delta trap when the flap was removed. Lure position within a delta trap did not affect moth catch, but it did affect the position of a moth's first contact with the trap. Lures placed high in the trap elicited moth landing on the inside surface of the trap's side or on the outside of the trap. Moths tended to land on the front flap when lures were placed in the adhesive. The relative field performance of traps in a sex pheromone-treated apple orchard was consistent with the flight tunnel studies, however, it was also influenced by moth population density. The 1CP trap caught significantly fewer moths than the other traps in an orchard with low codling moth density. The mean cumulative moth catch of each trap type was proportional to its adhesive-treated surface area within orchards receiving releases of sterile moths.

**Key words:** codling moth, traps, monitoring, mating disruption, sex pheromones

## INTRODUCTION

Traps baited with codlemone, the major sex pheromone component of codling moth, *Cydia pomonella* L. (Roelofs *et al.* 1971), have been used for > 25 yr to monitor populations in tree fruit orchards (Butt *et al.* 1974, Maitlen *et al.* 1976). Cumulative male catches in traps have been used to establish action thresholds for insecticide usage (Madsen and Vakenti 1972, Madsen *et al.* 1974, Riedl and Croft 1974) and as an indicator of phenology (Riedl *et al.* 1976, Beers and Brunner 1992). Moth catch has also been used to evaluate the success of mating disruption in orchards treated with sex pheromone (Vickers and Rothschild 1991).

The efficacy of a variety of trap types has been evaluated for codling moth in field trials (earlier work summarized in Riedl *et al.* 1986, Knodel and Agnello 1990, Vincent *et al.* 1990, Kehat *et al.* 1994). Traps have typically been constructed with inexpensive and disposable cardboard or plastic materials and have had a variety of shapes including cylindrical, delta, diamond and wing-style. Both disposable, sticky and reusable, non-sticky trap designs have been tested and compared (Knodel and Agnello 1990, Vincent *et al.* 1990). A synthesis of this work led to the suggestion and partial implementation of a standard protocol for monitoring codling moth with traps and lures (Riedl *et al.* 1986). The use of a wing trap with a notched bottom liner (Pherocon 1CP) baited with a red rubber septum loaded with 1.0 mg codlemone has been the mostly widely used monitoring system in the western U.S. during the 1980's and 1990's (Riedl *et al.* 1986, Gut and Brunner 1998).

The adoption of sex pheromone dispensers for mating disruption of codling moth occurred relatively rapidly during the 1990's in apple and pear orchards of Washington, California, and British Columbia, Canada. A prerequisite for the adoption of this new technology was the need to develop more intensive monitoring programs. Recommendations for monitoring included the use of a higher density of traps to detect potential problem areas within orchards and baiting traps with lures containing higher loads of pheromone to minimize the occurrence of "false negatives" in moth counts (Gut and Brunner 1996). The increased importance of monitoring in sex pheromone-treated orchards also led to the use of new trap designs including a larger delta trap and a new diamond-shaped trap. Unfortunately, the variability in the physical characteristics of these traps has hindered the implementation of a standardized protocol for monitoring codling moth and has created uncertainty among pest managers interpreting moth catches (Knight and Christianson 1999). To date, a comparison of these traps' performances for codling moth has not been reported.

Optimizing trap design is vital in developing a useful monitoring system. Slight changes in trap design can modify the pheromone plume structure and strongly affect moth flight and landing responses to a trap (Lewis and Macaulay 1976). Typically for most pest species, trap designs have been compared in a non-systematic, *ad hoc* approach without regard to understanding the effect of their individual features on moth behavior (Phillips and Wyatt 1992). Conversely, controlled studies of moth behavior in flight tunnels have proven to be useful in improving trap designs (Foster and Muggleston 1993, Foster *et al.* 1995). A study of codling moth's response to traps under controlled conditions in a flight tunnel has not been reported. Here we compare codling moth's behavioral response to four trap designs. In addition, the field performances of these traps were compared under low and high moth densities in trials conducted within apple orchards treated with sex pheromone dispensers for mating disruption.

## MATERIALS AND METHODS

**Trap types.** Studies were conducted with several paper and plastic trap types manufactured by Trécé Inc. (Salinas, CA) that are commonly used in tree fruits in the western United States: the delta trap, Pherocon VI; the diamond trap, Pherocon IIB; and the wing style traps, Pherocon 1C and Pherocon 1CP**.** The four traps vary in their overall geometries but have similar exterior dimensions, except for the smaller IIB diamond trap (Table 1). The two wing traps differ with regard to their bottom piece. The two pieces of the 1C wing trap are separated by a 5 cm plastic spacer and are the same size. The bottom wing in the 1CP wing trap is smaller and fits underneath the upper wing. The primary opening of the 1CP wing trap is a 4.0 x 5.6 cm notch cut in the center edge of the bottom piece. The area of the four traps' interior surfaces coated with adhesive was not related to a trap's exterior dimensions. The smaller IIB diamond trap has the largest area coated with adhesive; however, only 50% of this treated surface is situated on the bottom of the trap. The 1C wing trap has the largest horizontal adhesive-treated surface area and the 1CP wing trap has the smallest surface area. Interestingly, the percentage of the horizontal surface that is effectively covered with adhesive varied among traps. The bottom surface of the IIB diamond trap is the only trap completely covered with adhesive. The other three traps have 23 - 48% of their inside bottom surface left untreated (Table 1). The ratio of nonsticky to sticky surfaces varies among traps, primarily due to the variability in the exterior size of the traps and because all three inside surfaces of the IIB diamond trap are treated with adhesive. Both the VI delta and the IIB diamond traps have front flaps (flap height is about 3.0 cm) that are not treated with adhesive. The area and maximum height of three of the trap's openings are similar. However, the opening of the 1CP wing trap is only half as large as the other traps (Table 1).

**Table 1.**

Physical characteristics of the Pherocon traps (Trécé Inc., Salinas, CA) evaluated in this study

| | Trap type | | | |
|---|---|---|---|---|
| Trap characteristics | VI delta | IIB diamond | 1C wing | 1CP wing |
| Exterior dimensions (cm) length by width | 27.0 x 20.0 | 17.8 x 16.5 | 26.0 x 22.0 | 26.0 x 22.0 |
| Area ($cm^2$) of adhesive-covered bottom inside surface | 420.0 | 248.7 (497.4) [a] | 409.4 | 227.3 |
| % inside trap bottom covered with adhesive | 87.3 | 100.0 | 64.1 | 51.7 |
| Ratio of non-sticky to sticky trap surfaces | 6.9 | 1.7 | 5.2 | 8.5 |
| Height (cm) of front flap | 3.3 | 1.5 – 3.0 | - | - |
| Area ($cm^2$) of trap opening | 42.8 (8.0)[b] | 48.0 (7.0) | 42.7 (5.0) | 26.5 (2.5) |

[a] Value in parentheses is the area of all interior surfaces covered with adhesive.

[b] Value in parentheses is the maximum height of the trap's opening (cm).

**Flight Tunnel Studies**. The flight tunnel was constructed from 6 mm acrylic sheeting (1.66 m long, 0.57 m wide and 0.57 m high). A 12-volt DC blower was used to pull air from the room (maintained at 22-24 °C and 50-60% RH) into a plenum, through a charcoal filter, and through a series of screens before passing into the tunnel. Air flow through the tunnel was maintained at 0.25 m/sec. Exhaust was expelled to the outside of the building. Red lights installed above the tunnel provided enough light (4.3 lux) to make behavioral observations. Traps were placed on a ring stand 0.31 m above the tunnel floor and 0.20 m from the entrance of the tunnel. Traps were baited with a halobutyl gray septum loaded with 0.1 mg codlemone. Lures were pinned to the middle of the trap bottom and above the adhesive in all traps, except in the study that evaluated the effect of lure position.

Male moths ( < 36 h old) were obtained from the USDA laboratory colony reared on artificial diet, and conditioned in constant light for 24 - 48 h at 21 °C and 60% RH. Prior to testing, moths were placed in complete darkness for 30 min then released from a 30 cm high platform placed near the air outlet end of the tunnel. Individual moths were flown to traps and moth behavior was recorded for 6 min or until the moth was caught in the trap. New traps were used after each replicate.

The first study compared moth's responses to each trap type. Trap order was randomized on each day. Five moths (18 replicates) were flown consecutively to each trap type. The occurrence of wing fanning, upwind anemotactic flight, landing on the trap, entering the trap, and capture were recorded for each moth for the first six replicates. Data were also recorded for the position of first moth contact with the trap for the last 12 replicates. The location of first moth contact with the trap was summarized into three categories: landing on the outside of the trap, landing on the opening of the trap, or flying inside the trap. Moths landing on the front flaps of the IIB and VI traps were scored as landing on the front opening.

Two additional studies were conducted in the flight tunnel to evaluate specific features of the trap / lure system. The first test evaluated the response of males to both the IIB and the VI traps with and without front flaps. Flaps were removed with a razor blade. Forty moths were flown to each of these four trap types using the same experimental procedure (the order of traps was randomized each day and five moths were flown consecutively for 6 min to each trap). Eight replicates were run with each trap. The occurrences of wing fanning, upwind anemotactic flight, landing on the trap, entering the trap, capture, and the position of first contact on the trap were recorded for each moth. The second test evaluated the effect of lure position within the VI delta trap on capture efficiency. Three lure positions within the trap were compared: pinned to the top center, pinned to the bottom center, and pinned to the bottom side. The occurrences of wing fanning, upwind anemotactic flight, landing on the trap, entering the trap, capture, and the position of first contact on the trap were recorded for each moth. Forty moths were flown to traps with each lure position using the same experimental procedure described above.

**Field trials**. Two field tests were conducted to evaluate the performance of the four trap types in apple orchards treated with sex pheromone dispensers (1,000 Isomate C+ dispensers per ha, Pacific Biocontrol, Vancouver, WA). Fifteen traps of each of the four trap types were randomly spaced 20 m apart in an 18 ha 'Red Delicious' orchard near Moxee, WA in test 1. Trap height was standardized at 3.0 m in the canopy (mean (SE) tree height averaged 4.1 (0.1) m). The test was conducted from 17 April to 4 May 1998. Test 2 was conducted from 20 August to 9 September 1998 in a nearby 14 ha 'Red Delicious' orchard. Trap height was standardized at 3.0 m in the canopy (mean (SE) tree height averaged 4.2 (0.1) m). Ten replicates of each trap type were randomized within the orchard and spaced 20 m apart. Five thousand sterile codling moths (50:50 male: female ratio) obtained from the Sterile Insect Release Program (Osoyoos, British Columbia) were released into this orchard just prior to the start of the study and again on 27 August and 3 September. Sterilized moths were exposed to 33 krad of gamma radiation and stored at 2 °C for < 48 h prior to release. Moth catch in each trap was recorded every two days; however moths were not removed from traps during the test.

**Data analysis**. A multiple comparison test for proportions (Ryan 1960) was used to test for significant differences ($P = 0.05$) among trap types in the behavioral response of moths (orientation to the trap, trap contact, and moth capture) in the flight tunnel tests. Ryan's test was also used to test for differences among traps for the proportion of moths first contacting a given position on the trap (outside, front opening, and inside) and for each position's capture efficiency. Fisher's exact test (2 x 2 contingency table) was used to compare the proportion of moths captured in tests evaluating the delta and diamond traps with and without front flaps. Chi-square analysis was used to compare the frequency distribution of moth contact in delta traps with lures placed at three positions within traps. All moth counts in field trials were transformed with square root (x + 0.01) and tested with analysis of variance (PROC GLM, Hintze 1987). Means were separated in significant ANOVA's with Fisher's least significance difference (Hintze 1987).

## RESULTS

**Flight Tunnel Studies.** No difference in the proportion of moths orienting to or touching the traps was found among traps (Table 2). However, the proportion of moths touching the 1CP wing trap that were caught was significantly lower than for the 1C wing and IIB diamond traps. The proportion of moths tested that were trapped was significantly lower with the 1CP wing versus the IIB diamond trap.

The distribution of moth contacts with traps and the proportion of moths captured varied among traps (Table 3). A significantly higher proportion of moths first contacted the wing traps on the outside of the traps versus the VI delta and IIB diamond traps. The proportion of moths landing on the outside of the VI delta trap that was eventually caught in the adhesive was significantly lower than with the 1C wing trap. A significantly lower proportion of moths contacting the wing traps landed on the opening of the trap versus the proportion landing on the flaps of the IIB diamond and VI delta traps. Capture efficiency for these moths was significantly lower for the 1CP than the other traps. No significant difference was found among traps for the proportion of moths that flew directly into the trap though nearly 3-fold more moths flew into the VI delta than the wing traps. The capture rate for moths flying into all four traps was > 72%. Moths entering the IIB diamond trap avoided the two adhesive-covered upper sides and were never caught on their surfaces.

**Table 2.**

Flight tunnel response of codling moth males to traps baited with a grey septa loaded with 0.1 mg codlemone, n = 30.

| | Proportion of moths | | | |
|---|---|---|---|---|
| Trap type | Released that oriented to trap | Orienting that contacted trap | Contacting trap that were caught | Released that were caught |
| VI Delta | 0.77a | 1.00a | 0.82ab | 0.62ab |
| IIB Diamond | 0.73a | 1.00a | 0.96a | 0.70a |
| 1C Wing | 0.70a | 0.95a | 0.95a | 0.63ab |
| 1CP Wing | 0.70a | 0.90a | 0.74b | 0.47b |

Column proportions are not significantly different if followed by the same letter, $P < 0.05$; Ryan's (1960) multiple comparison test for proportions.

**Table 3.**

Distribution of male codling moths' first contact with several trap types baited with 0.1 mg codlemone and the success of moth capture for each trap location in flight tunnel tests (n=6).

| | Number of moths contacting trap | Proportion of moths first contacting[1]: | | | | | |
|---|---|---|---|---|---|---|---|
| | | Outside of trap | | Front opening of trap | | Flying inside trap | |
| Trap type | | Landing | Captured | Landing | Captured | Landing | Captured |
| Pherocon VI Delta | 50 | 0.10b | 0.10b | 0.56a | 0.83a | 0.34a | 0.94a |
| Pherocon IIB Diamond | 41 | 0.10b | 0.25ab | 0.63a | 0.81a | 0.27a | 0.73a |
| Pherocon 1C Wing | 34 | 0.56a | 0.58a | 0.32b | 0.82a | 0.12a | 0.75a |
| Pherocon 1CP Wing | 36 | 0.56a | 0.30ab | 0.31b | 0.55b | 0.14a | 0.80a |

Column proportions are not significantly different if followed by the same letter, $P < 0.05$; Ryan's (1960) multiple comparison test for proportions.

[1] All moths touching each trap type were scored as having landed on one of three areas (proportions sum to 1.0). The proportion of moths touching each area that were subsequently captured is summarized in the table under 'Captured'.

The presence or absence of a front flap in either the VI delta or IIB diamond trap did not affect moth capture rates ($X^2 = 0.56$, df = 1, $P = 0.46$; $X^2 = 0.44$, df = 1, $P = 0.51$, respectively). However, the location of moth contact was significantly different in the VI delta traps with or without flaps ($X^2 = 8.96$, df = 2, $P < 0.01$) but not with the IIB diamond trap ($X^2 = 2.74$, df = 2, $P = 0.25$). Removal of the flap in the VI delta trap increased the proportion of moths that flew directly into the trap versus landing on the front of the trap and walking in.

Lure position did not affect the efficiency of moth capture in VI delta traps ($X^2 = 2.19$, df = 2, $P = 0.24$), however it did affect the distribution of moth contact with the trap ($X^2 = 10.04$, df = 2, $P < 0.01$). When the lure was pinned to the interior top of the trap a majority of moths flew into the trap and first landed on the inside top surface before falling down onto the adhesive. In contrast, a majority of moths first landed on the front flap and walked into traps when the lure was pinned to the center or side of the interior bottom of the trap.

**Field trials**. Significant differences in moth catch occurred among traps during both field tests (Table 4). Test 1 was conducted in the spring during the first flight of codling moth and few moths were caught in traps. Mean moth catch was significantly lower in the 1CP wing trap versus the other three traps. Test 2 was conducted later in the season and moth catch was > 10-fold higher in this test than during the spring trial due to the high number of moths released into the orchard ( > 90% of moths captured were released sterile moths based on the presence of a red internal dye). The IIB diamond and 1CP wing traps with the smallest adhesive-treated surfaces caught significantly fewer moths than the larger VI delta and 1C wing traps in this test. The rate of catch over time leveled off for each trap due to saturation of the adhesive-treated surfaces (Fig. 1). Cumulative catch in both the IIB diamond and 1CP wing traps saturated at about 40 moths per trap (Fig. 1). Cumulative moth catch saturated at a higher level in the VI delta than the 1C wing trap despite having a nearly 30% smaller adhesive-treated surface area (Fig. 1, Table 1).

**Table 4.**

Comparison of male codling moth catch in several trap types baited with 10 mg codlemone red septa within a sex pheromone-treated apple orchard

| | Mean (SE) moth catch per trap | |
|---|---|---|
| Trap type | Test 1[a] | Test 2[b] |
| Pherocon VI Delta | 6.3 (0.9)a | 93.9 (9.5)b |
| Pherocon IIB Diamond | 6.4 (1.7)a | 39.6 (2.2)a |
| Pherocon 1C Wing | 6.6 (1.4)a | 77.6 (5.7)b |
| Pherocon 1CP Wing | 3.0 (0.7)b | 40.8 (4.6)a |
| Statistical test | $F_{3,53} = 5.15$ $P < 0.05$ | $F_{3,35} = 24.7$ $P < 0.001$ |

[a] This test was conducted from 17 April to 4 May 1998.

[b] This test was conducted from 20 August to 9 September 1998. The orchard was treated with three releases of 5,000 sterile moths.

## DISCUSSION

Codling moth is a direct pest of pome fruit and typically occurs at low densities in commercial orchards. For example, the action thresholds established for moth catch in sex pheromone-baited traps are usually < 5 moths per week (summarized in Riedl *et al.* 1986). Three of the four traps tested in our field study performed similarly in an orchard with a low to moderate population density of codling moth. At higher moth densities, the area of a trap's adhesive-treated surface was an important factor affecting catch. Riedl (1980) found that a density of > 0.2 moths per $cm^2$ of adhesive-treated surface reduced subsequent codling moth captures in sticky traps. Data from our study was consistent with this estimate (Fig. 1, Table 1). However, other factors, such as visual cues can play a role in the capture efficiency of a trap (Foster et al. 1991). Male *E. postvittana* flying into traps with moths already captured, landed closer to the sex pheromone lure than in clean traps. The influence of previous moth captures within a trap on the orientation and landing behavior of codling moth has not been addressed.

Saturation of sticky traps with moths is a common problem in monitoring tortricid orchard pests that occur at high densities, such as tortricid leafrollers (Brown 1984, Knight 2001). However, our data suggest that saturation is not a factor in any of these trap types when the

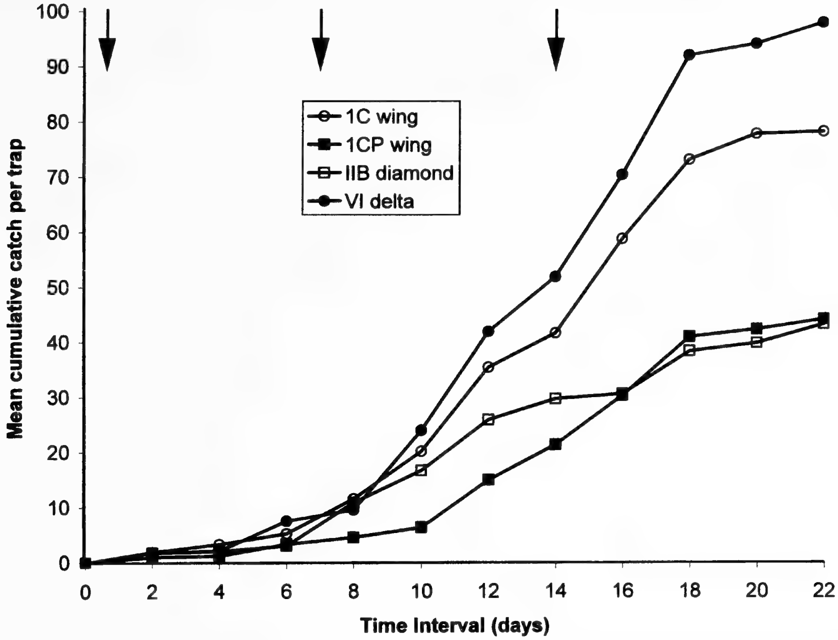

**Figure 1.** Cumulative catch of codling moth males from 20 August to 9 September 1998 in four trap types placed in a 14-ha apple orchard. Five thousand sterilized codling moths were released in the orchard on 20 August on the first day of the test and again on 27 August and 3 September (release dates indicated by vertical arrows).

cumulative moth catch is < 20 moths. Therefore, current recommendations for codling moth trap maintenance should be adequate, especially in sex pheromone-treated orchards if trap liners are replaced frequently (Riedl *et al.* 1986).

Surprisingly, the Pherocon 1CP wing trap performed poorly in both our flight tunnel and field tests. Previous field trials have reported that the 1CP wing trap was very effective (Charmillot *et al.* 1975) and this trap has been widely used to monitor codling moth in the western United States (Gut and Brunner 1998). However, in our flight tunnel tests the 1CP wing trap was the least effective among the four traps tested in capturing moths after they contacted the trap. In particular, a low proportion of moths landing on the front of the trap were captured. The low efficiency of the 1CP wing trap was apparently due to the absence of adhesive on either side of the center notch on the bottom liner. Qualitative physical evaluations of various 1CP wing traps produced by several manufacturers over the last 15 yr suggest that traps vary tremendously in the deposition of adhesive. Our data suggest that this variability would have a significant impact on the relative performance of these traps.

The presence of a front flap in a trap has been suggested to serve as an effective barrier restricting the ability of moths to exit the trap. Riedl (1986) cited unpublished data that the flap in a diamond-shaped trap increased catch of codling moth. The inclusion of a front barrier in the IOBC cylinder trap significantly increased catch of codling moth (Charmillot *et al.* 1975). Foster and Muggleston (1993) in a flight tunnel test with *Epiphyas postvittana* (Walker) found that the front flap on a delta trap increased the proportion of moths entering the trap that were caught. Interestingly, they also found that the height of the flap influenced the moth's landing position on the adhesive and the catch efficiency of the trap. Higher flaps caused the moths to land further upwind and farther from the trap's exit. Flight tunnel studies with *Ctenopseustis obliquana* (Walker) showed that removing the front flap from a delta trap increased the proportion of moths that entered the trap but also increased the proportion of moths that escaped (Foster *et al.* 1995). The flaps in the diamond and delta traps did not play a significant role in capturing codling moth in our tests. However, we hypothesize that the presence of the flap in the VI delta trap may be responsible for retaining a higher number of moths compared with the IC wing trap in our field tests.

Plume structure and species-specific flight behaviors can influence the effectiveness of trap designs. Clearly, the responses of codling moth we observed to traps placed in clean air in a flight tunnel may or may not be consistent with its' responses to traps placed in an orchard treated with sex pheromone dispensers. Comparative behavioral studies in a flight tunnel of the leafrollers, *Planotortrix octo* (Dugdale) and *E. postvittana* found that the former species was more sensitive to its pheromone plume structure. When delta traps were placed at increasing angles to the wind direction moth orientation and capture of only *P. octo* declined (Foster *et al.* 1991). The wide inter-track reversal distances during anemotactic flight of *C. obliquana* reduced the effectiveness of delta traps (Foster *et al.* 1995). A large proportion of these moths landed on the outside of the trap and lost contact with the plume. Conversely, we found that only a low proportion of codling moths landed on the outside of the VI delta trap; however, a significantly lower proportion of these moths were captured compared with the other trap types. Foster *et al.* (1995) improved the delta trap performance for *C. obliquana* by increasing the pheromone dose of the lure, which decreased the flight tracking angles. They also found that by using a rectangular trap moth capture was improved versus the delta trap with its narrow apex. A rectangular trap design has not been tested for codling moth nor has the influence of lure dosage on male anemotactic flight been reported.

Lure placement within a trap can be an important factor affecting moth capture. The efficiency of the delta trap for *E. postvittana* was increased when the lure was placed at the side of the adhesive-treated bottom surface versus the center or higher in the trap (Foster *et al.* 1991). However, lure placement did not affect the proportion of moths orienting to the trap. In comparison, lure placement in the VI delta trap in our study with codling moth did not affect either capture efficiency or moth orientation. Similarly, McNally and Barnes (1980) reported that there was no difference in the catch of codling moth in a 1C wing trap whether the lure was placed high or low in the trap.

Sex pheromone-baited traps play a critical role in monitoring codling moth in orchards treated with sex pheromone for mating disruption. Trap and lure use have been modified since 1990 when the first pheromone dispensers were registered, to reflect the orchard manager's need to assess moth population density in disrupted-orchards more than to measure the level of disruption in the orchard (Gut and Brunner 1996). Traps are positioned within the orchard and within the canopy to enhance their ability to capture moths, e.g. orchard borders (Knight and Christianson 1999), upper canopy (Knight 1995, Barrett 1995), and distant from pheromone dispensers (Knight *et al.* 1999). Standardization of these factors, as well as trap and lure type, will likely improve monitoring of codling moth. Our data suggest that the currently used delta, diamond, and wing style (1C) traps are equally effective in capturing codling moth at low to moderate moth densities. Proper maintenance of these traps' adhesive surfaces is one factor that can be controlled to improve monitoring of codling moth.

## ACKNOWLEDGEMENTS

We would like to thank Bill Lingren (Trécé Inc., Salinas, CA) for providing the traps and lures and Ken Bloem (Sterile Insect Release Program, Osoyoos, British Columbia) for providing the sterile codling moths. The paper was strengthened by the helpful comments made by Eugene Miliczky (USDA, ARS, Wapato, WA), Bruce Barrett (Univ. of Missouri, Columbia, MO), and Mark Brown (USDA, ARS, Kearneysville, WV). This research was partially funded by the Washington Tree Fruit Research Commission, Wenatchee, WA.

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# α-Pinene and ethanol: Key host volatiles for *Xylotrechus longitarsis* (Coleoptera: Cerambycidae)

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## ABSTRACT

*Xylotrechus longitarsis* Casey is a common wood-boring beetle that causes considerable losses to the softwood lumber industry in British Columbia. Trapping experiments were conducted in the southern interior of British Columbia to determine whether the generic bait of α-pinene plus ethanol is an optimal combination for attraction of *X. longitarsis*. α-Pinene alone attracted substantial numbers of *X. longitarsis* and trap catches were increased significantly with the addition of ethanol lures but different release rates of ethanol had no significant effect. The blend of pure α-pinene and ethanol was significantly more attractive than more complete blends of conifer monoterpenes and ethanol, whether or not α-pinene was a major component of the blend. Strong attraction to α-pinene reflects the preference of *X. longitarsis* for conifers, and particularly Douglas-fir, *Pseudotsuga menziesii* (Mirbel) Franco, the bark of which is relatively rich in α-pinene. Increased attraction with the addition of ethanol lures, irrespective of release rates, to traps baited with α-pinene suggests that *X. longitarsis* prefers severely stressed hosts or deteriorating host material but may also utilize freshly cut or broken material.

**Key words:** *Xylotrechus longitarsis*, Cerambycidae, chemical ecology, host volatiles, woodborers, pest management, trapping

## INTRODUCTION

*Xylotrechus longitarsis* Casey is a coniferophagous wood-boring beetle that is common and widespread in British Columbia (BC), ranging east into Alberta and south to Colorado and northern California (Linsley 1964). The flight period is reported as May to August

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(Linsley 1964) but adults may be abundant well into September in the southern interior of BC, where this species is usually the most numerous of the large wood-boring insects (Cerambycidae, Buprestidae, Siricidae) captured around log storage areas (McIntosh *et al.* 2001; Morewood *et al.* 2002). The relative abundance of *X. longitarsis* suggests that it is a major contributor to the estimated $43.6 million (US) in annual degrade losses to the softwood lumber industry caused by large woodborers in the interior of BC (Phero Tech Inc. 1997).

Wood-boring insects are pests of timber destined for lumber production, attacking and degrading dead or dying trees and logs after harvest but before processing. Management of large woodborers has been limited primarily to a strategy of preventing attack through rapid utilization, peeling, water sprinkling, or storage of logs in water or in compact decks with maximum shading (Safranyik and Moeck 1995), with operational trapping programs currently under development. In contrast, prevention of attack by ambrosia beetles (Coleoptera: Scolytidae) is accomplished in part through well-established trapping programs using semiochemical-baited traps (Borden 1995). Various combinations of host monoterpenes and ethanol are attractive to coniferophagous cerambycids (Ikeda *et al.* 1980; Fatzinger *et al.* 1987; Phillips *et al.* 1988), with some evidence that α-pinene is the most attractive of individual monoterpenes tested (Ikeda *et al.* 1986; Chénier and Philogène 1989). Currently, the simple combination of α-pinene and ethanol is used provisionally as a generic bait for trapping large woodborers in BC. However, this blend does not replicate the complex mixture of host-associated chemical cues that could be used by these insects during host selection. Our objective was to determine whether more complete blends of conifer volatiles, primarily monoterpenes and ethanol, would be more attractive to *X. longitarsis* than pure α-pinene and ethanol.

## MATERIALS AND METHODS

Different combinations of host volatiles were tested as baits in 12-unit multiple funnel traps (Lindgren 1983) suspended from metal poles with the top funnel about 1.5 m above ground. Captured insects were frozen until they could be sorted and counted.

To test whether ethanol is important in attracting *X. longitarsis* and whether such attraction is affected by release rate, an experiment was superimposed on operational trapping programs around the log storage yard at Gorman Bros. Ltd. in Westbank and the Riverside Forest Products Ltd. 4-Mile dryland log sort and Okanagan Lake log dump, both on the Bear Forest Service Road west of Kelowna. Traps were baited with α-pinene [96% (–) enantiomer, > 99% chemical purity, released at 2.2 g/d; Phero Tech Inc., Delta, BC] alone or combined with either low-release (30-50 mg/d) or high-release (1.8 g/d) ethanol lures in randomized complete blocks on 2 September 1999. Insects were collected from nine blocks of traps on 10 September 1999 and 12 blocks of traps on 17 September 1999, for a total of 21 replicates.

To test whether α-pinene is an adequate host-recognition cue for *X. longitarsis*, compared to more complete blends of conifer monoterpenes, two experiments were conducted in a small clearcut 8.3 km up the Laluwissen Forest Service Road north of Lytton. The surrounding forest was predominantly Douglas-fir, *Pseudotsuga menziesii* (Mirbel) Franco, with some lodgepole pine, *Pinus contorta* Douglas ex Loudon, and ponderosa pine, *Pinus ponderosa* P. & C. Lawson. In each experiment, catches in traps baited with a blend of host volatiles distilled from lodgepole pine turpentine (H.D. Pierce Jr., Department of Biological Sciences, Simon Fraser University, unpublished data) were compared to catches in traps baited with pure α-pinene (as above, release rate 150 mg/d) and to catches in unbaited traps, deployed in 10 randomized complete blocks. Both host blends and α-pinene were combined with low-release ethanol lures. In the first experiment, traps were baited with a modified host blend (released at 750 mg/d), with β-phellandrene enriched and α-pinene nearly eliminated (Table 1), on 1 August 2001 and insects were collected on 14 August 2001. In the second experiment, traps were baited with a natural host blend (released at 700 mg/d), distilled without greatly altering the relative proportions of major components (Table 1), on 28 August 2001. Insects were collected on 11 September 2001 and the treatments were re-randomized to minimize position effects. Insects were collected again on 23 September 2001 to compensate for the declining catches later in the season, and the two collections were combined for a total of 10 replicates.

**Table 1**

Composition of "natural" and "modified" host blends distilled from lodgepole pine turpentine and used in trapping experiments for *Xylotrechus longitarsis*.

| Compound | Enantiomeric composition (%) | | Percent of host blend | |
|---|---|---|---|---|
| | (+) | (−) | Natural | Modified |
| α-pinene | 44 | 56 | 18.4 | 0.9 |
| β-pinene | 0 | 100 | 16.6 | 4.4 |
| 3-carene | 100 | 0 | 23.6 | 24.8 |
| limonene | 42 | 58 | 3.8 | 7.8 |
| β-phellandrene | 0 | 100 | 28.0 | 51.0 |
| unidentified minor components | n.a. | n.a. | 9.6 | 11.1 |

Data were transformed by $\log(x + 1)$ to correct for non-normality and heteroscedasticity (Thöni 1967; Zar 1999) and then subjected to analysis of variance (PROC ANOVA) for randomized complete blocks (Kvanli 1988; SAS Institute Inc. 1999). Means were compared using the Ryan-Einot-Gabriel-Welsch (REGWQ) multiple range test (Day and Quinn 1989; SAS Institute Inc. 1999).

## RESULTS

Traps baited with α-pinene plus ethanol captured significantly greater numbers of *X. longitarsis* than traps baited with α-pinene alone ($F_{2,40} = 5.89$, $P = 0.0057$), but trap catches did not differ significantly between traps with ethanol released at high or low rates (Fig. 1).

Traps baited with α-pinene plus ethanol captured significantly greater numbers of both sexes of *X. longitarsis* than traps baited with ethanol plus either the modified host blend ($F_{2,18} = 16.06$, $P < 0.0001$ for males; $F_{2,18} = 38.06$, $P < 0.0001$ for females) or the natural host blend ($F_{2,18} = 19.82$, $P < 0.0001$ for males; $F_{2,18} = 11.54$, $P = 0.0006$ for females). Traps baited with either host blend captured significantly greater numbers of males, but not females, than unbaited traps (Fig. 2).

## DISCUSSION

The simple combination of α-pinene and ethanol appears to be particularly well-suited for attracting *X. longitarsis*, reflecting both host preferences and considerable flexibility with respect to suitable host material. The only host association published for *X. longitarsis* is Douglas-fir (Linsley 1964) and most of the reared specimens in the insect collection at the Pacific Forestry Centre, Victoria, BC, are from Douglas-fir. α-Pinene is the dominant monoterpene in Douglas-fir bark (D.S. Pureswaran, Department of Biological Sciences, Simon Fraser University, unpublished data) and is thought to be the primary attractant for the Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins (Coleoptera: Scolytidae) (Heikkenen and Hrutfiord 1965).

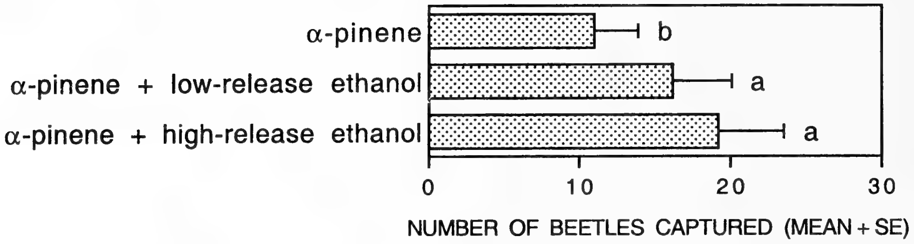

**Figure 1.** Catches of *Xylotrechus longitarsis* at three locations in the central Okanagan Valley, BC, 2-17 September 1999 in traps baited with α-pinene (released at 2.2 g/d) alone or combined with either low-release (30-50 mg/d) or high-release (1.8 g/d) ethanol lures. The difference between the bars with the same letter is not statistically significant (REGWQ, $P > 0.05$).

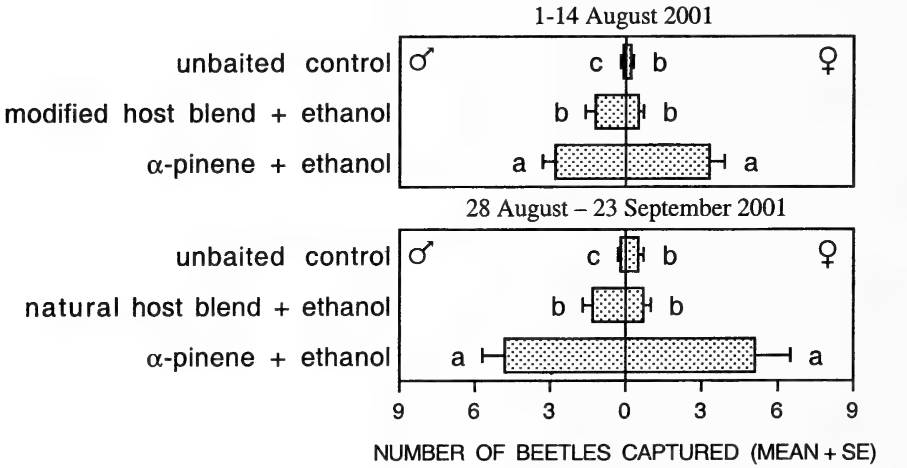

**Figure 2.** Catches of *Xylotrechus longitarsis* near Lytton, BC, in August and September 2001 in traps baited with a modified (above) or natural (below) host blend (released at 750 mg/d or 700 mg/d, respectively) or α-pinene (released at 150 mg/d), each combined with ethanol (released at 30-50 mg/d), or unbaited. For a given time period and sex, differences between bars with the same letter are not statistically significant (REGWQ, $P > 0.05$).

On the other hand, the geographic range of *X. longitarsis* extends beyond that of Douglas-fir and other conifer species can serve as hosts. We have reared *X. longitarsis* in ponderosa pine bolts and there are specimens in the insect collection at the Pacific Forestry Centre reared from logs of lodgepole pine, western hemlock, *Tsuga heterophylla* (Rafinesque-Schmaltz) Sargent, western larch, *Larix occidentalis* Nuttall, and white spruce, *Picea glauca* (Moench) Voss. Despite this apparent broad acceptability of different conifer hosts, including lodgepole pine, monoterpene blends derived from lodgepole pine were significantly less attractive than pure α-pinene (Fig. 2). Furthermore, this lack of attraction was not simply due to the lack of α-pinene in the modified host blend because the natural host blend, which contained a substantial amount of α-pinene (Table 1) and released it at a rate of 129 mg/d (compared to 150 mg/d for the pure compound), was no more attractive relative to pure α-pinene than the modified host blend (Fig. 2). Coupled gas chromatographic – electroantennographic detection analyses indicate that the antennae of *X. longitarsis* can detect each of the five prominent monoterpenes listed in Table 1 (R.

Gries, Department of Biological Sciences, Simon Fraser University, unpublished data). These considerations suggest that some component of these natural host blends is either repellent to *X. longitarsis* or interferes with the response to α-pinene.

Like many cerambycid species that breed in severely stressed hosts (Hanks 1999), adult *X. longitarsis* are attracted to recently felled trees and cut logs. Ethanol is a primary attractant for other species that breed in recently felled trees and cut logs, such as the ambrosia beetles *Gnathotrichus sulcatus* LeConte and *Trypodendron lineatum* (Olivier) (Cade *et al.* 1970; Moeck 1970), and might be considered a general indicator of stress in trees (Kimmerer and Kozlowski 1982; Kelsey and Joseph 1998). Cut or broken conifers initially release large amounts of monoterpenes, with gradually increasing amounts of ethanol as the material deteriorates, and many bark and ambrosia beetles and their associates are attracted to ratios of α-pinene and ethanol that reflect the condition of host material to which each species is adapted (Schroeder and Lindelöw 1989). In contrast, *X. longitarsis* would appear to accept host material in a broad range of conditions, considering the similarity of catches in traps with very different release rates of ethanol and the substantial catches even in traps baited with α-pinene alone (Fig. 1).

For operational trapping, the simple combination of α-pinene and ethanol appears to be optimal for attracting *X. longitarsis* and also has economic and practical advantages over more complete monoterpene blends. A lure containing a single compound is likely to be less expensive than one with a more complex blend and α-pinene is more easily purified than other conifer monoterpenes (H.D. Pierce Jr., personal communication). In addition, blends containing large amounts of β-phellandrene are unpleasant to work with because β-phellandrene is unstable and tends to polymerize on the outside of the lures as it is released, creating a sticky mess.

## ACKNOWLEDGEMENTS

We thank Hugh Norman (BC Chemicals, Prince George, BC) for the generous gift of lodgepole pine turpentine, Nick Arkle (Gorman Bros. Ltd.), Gary Greyell (Riverside Forest Products Ltd.), and Ed Senger (BC Ministry of Forests) for access to field sites, and Bob Duncan for access to the insect collection at the Pacific Forestry Centre. Financial support was provided by Forest Renewal British Columbia, the Science Council of British Columbia, the Natural Sciences and Engineering Research Council of Canada, Abitibi Consolidated Forest Products Inc., Ainsworth Lumber Co. Ltd., British Columbia Hydro and Power Authority, Bugbusters Pest Management Inc., Canadian Forest Products Ltd., Gorman Bros. Ltd., International Forest Products Ltd., Lignum Ltd., Manning Diversified Forest Products Ltd., Millar Western Forest Products Ltd., Phero Tech Inc., Riverside Forest Products Ltd., Slocan Forest Products Ltd., Tembec Forest Industries Ltd., TimberWest Forest Corp., Tolko Industries Ltd., Weldwood of Canada Ltd., West Fraser Mills Ltd., Western Forest Products Ltd., and Weyerhaeuser Canada Ltd.

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# A Comparison of Gray Halo-butyl Elastomer and Red Rubber Septa to Monitor Codling Moth (Lepidoptera: Tortricidae) in Sex Pheromone-Treated Orchards

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## ABSTRACT

The emission rate, isomeric stability, and relative attractiveness of field-aged gray halo-butyl elastomer and red rubber septa loaded with 4.0 and 10.0 mg of (*E,E*)-8,10-dodecadien-1-ol (E8,E10-12:OH, codlemone), the major sex pheromone component for codling moth, *Cydia pomonella* L., were evaluated. Initially, field-aged red septa loaded with 10.0 mg had significantly higher emission rates than gray septa loaded with 4.0 mg codlemone. Emission rates of codlemone decayed over time from both lures and were similar for lures aged 28-42 d in the field. Isomerization of E8,E10-12:OH occurred rapidly in red septa but did not occur in the gray septa. Moth capture in traps baited with either lure type aged in the field did not differ initially (0 and 7 d), but were significantly lower in traps baited with 14, 28, and 42 d-old red versus gray septa. Significant differences observed in the attractiveness of these two types of field-aged lures were primarily due to changes in their isomeric purity and not to differences in their emission rate. Increasing the codlemone load of gray septa up to 20.0 mg did not improve the performance of lures in sex pheromone-treated orchards. All lures were effective for 10 wk. Loading gray septa with 50.0 mg codlemone increased lure attractiveness and extended its longevity to 16 wk. Proprietary gray septa loaded with a high rate of pheromone and replaced once per season were more attractive than the standard 10.0 mg loaded red septa replaced three times in a sex pheromone-treated orchard.

**Key words**: *Cydia pomonella*, codling moth, sex pheromone, monitoring, lures

## INTRODUCTION

Codling moth, *Cydia pomonella* L., is the major direct pest of pome fruits and walnut throughout the world (Shel'deshova 1967). Following the identification of the sex pheromone of codling moth, (*E,E*)-8,10-dodecadien-1-ol (E8, E10-12:OH, codlemone) (Roelofs *et al.* 1971), moth catches in pheromone baited traps have been widely used to establish action thresholds (Riedl and Croft 1974) and to track the seasonal timing of key population events (Riedl *et al.* 1976). Traps baited with red rubber septa impregnated with codlemone have been the most widely used dispenser system (Riedl *et al.* 1986). Lure loadings between 0.1 and 1.0 mg codlemone have provided optimal attraction (Maitlen *et al.* 1976, Culver and Barnes 1977, McNally and Barnes 1980, Kehat *et al.* 1994).

Maitlen *et al.* (1976) characterized the first-order release characteristics of codlemone from red rubber septa under controlled laboratory conditions (23 °C). Based on both analytical and biological studies they determined that a 1.0 mg lure should maintain a maximum level of attraction for up to four wk. Their calculations suggested that a 5.0 mg loading would remain effective for >4 months. Riedl *et al.* (1986) used the half-life calculations of Maitlen *et al.* (1976) to predict that red rubber septa loaded initially with 1.0 mg codlemone should be effective for up to 11 wk (based on maintaining a residual pheromone content >0.1 mg). This predicted long field-life of the red rubber septa was demonstrated by McNally and Barnes (1980). Field-aged lures loaded with 1.0 mg codlemone were equally effective as new lures for up to 16 wk. However, Culver and Barnes (1977) found that the attractiveness of 1.0 mg lures dropped significantly after 2-3 wk in the field. Riedl *et al.* (1986) hypothesized that this large difference observed in the longevity of field-aged red rubber septa might be due to changes in the manufacturer's formulation. Subsequent field studies found that both the emission rate and the attractiveness of red rubber septa declined rapidly after two wk (Kehat *et al.* 1994).

Concurrent with the rapid adoption of sex pheromone dispensers for mating disruption of codling moth during the 1990's was the use of monitoring lures loaded with higher rates of codlemone (Charmillot 1990). Red rubber septa loaded with 10.0 mg codlemone have been the most common lure used in sex pheromone-disrupted orchards in western North America (Knight 1995a, Judd *et al.* 1996, Gut and Brunner 1998). Lures with high loads of codlemone have allowed pest managers to track the population density and phenology of codling moth within sex pheromone-treated orchards. Current monitoring recommendations of sex pheromone-treated orchards with 10.0 mg red septa suggest changing lures every 2-3 wk (Gut and Brunner 1996). The short life of these high load lures was hypothesized to be due to the depletion of codlemone under high summer temperatures (Gut and Brunner 1995), similar to the results reported from Israel with standard lures (Kehat *et al.* 1994). This frequent replacement schedule for lures combined with a higher density of traps has increased the cost of monitoring sex pheromone-treated orchards relative to conventional orchards (Knight 1995a).

The chemical instability of many sex pheromones can severely limit the longevity of lures (House *et al.* 1998). The chemical sensitivity of codlemone, a conjugated diene alcohol, to heat, light, and air is particularly acute (Brown and McDonough 1986, Ideses and Shani 1988). Several biochemical pathways can degrade codlemone, including isomerization and oxidation to peroxides and furans (Millar 1995). Rapid isomerization of codlemone within rubber septa is catalyzed by the presence of sulphur and sunlight (Brown and McDonough 1986). Isomerization of codlemone within sulphur-cured rubber septa begins immediately (Vrkoč *et al.* 1988), and the three isomers may account for 20% of the content within seven days in field-aged lures placed within traps (Brown and McDonough 1986). Chemical protection of codlemone can be accomplished with the addition of UV stabilizers and antioxidants (Ideses and Shani 1988, Millar 1995) or by the use of other lure substrates. For example, the isomerization of codlemone was 4.7 fold slower within phenolic resin-cured, gray halo-butyl elastomer lures versus the red rubber septa (Brown and McDonough 1986).

The isomeric purity of codlemone is an important factor affecting a lure's performance. Various crude mixtures of the three geometrical isomers of codlemone decreased the attractiveness of codlemone when incorporated together within red rubber septa-baited traps (Roelofs *et al.* 1972). A chemical equilibrium blend of the four isomers (61% *EE,* 5% *ZZ*, 14% *ZE*, and 20% *EZ*) significantly reduced the flight response of males in flight tunnel tests versus pure codlemone (McDonough *et al.* 1993). El-Sayd *et al.* (1998) found that the single addition of the *Z,E* isomer to codlemone synergized the response of codling moth in a flight tunnel, but moth capture in traps was not affected in a subsequent field study. In contrast, the addition of 20% *E,Z* isomer strongly depressed male responses both in a flight tunnel and to traps placed in the field.

The objective of this study was to evaluate the effects of emission rate and isomeric purity of codlemone on the attractiveness of lures for codling moth. Herein are reported the emission rate and isomeric purity of field-aged red rubber and gray halo-butyl elastomer septa. The relative attractiveness of lures was evaluated in a series of field trials within sex pheromone-treated apple orchards. Subsequent field tests evaluated the optimal loading rate of gray septa for season-long monitoring of codling moth in sex pheromone-treated orchards.

## MATERIALS AND METHODS

**Preparation of lures**. Gray halo-butyl elastomer septa (No. 1888, size No. 1) and red, natural rubber septa (No. 1171, size 1F) were used in all tests (West Co., Phoenixville. PA). Septa were extracted in hexane for 24 h, dichloromethane for another 24 h, and then air-dried for 48 h prior to loading. E8,E10-12:OH (97% purity, Aldrich Chemical, Minneapolis, MN) was added to the cup portion of the septa in a 200-$\mu$l aliquot of dichloromethane, followed by another 200 $\mu$l of dichloromethane to ensure penetration of the material. Initial studies found that a maximum of 4.0 mg codlemone could be loaded in gray septa using this technique. Codlemone crystallized on the surface of these lures at higher loadings. Thus, red and gray septa were loaded with 10.0 and 4.0 mg E8,E10-12:OH, respectively. Septa were kept frozen at –15 °C prior to use.

**Evaluation of field-aged septa.** Prepared septa were field-aged by pinning lures inside of non-sticky Pherocon IC wing traps (Trécé Inc., Salinas, CA) hung at 2.0 m height in the canopy of an unsprayed apple orchard (Yakima, WA). Eight septa of one type were placed 4.0 cm apart inside of traps, and pinned 1.5 cm above the traps' bottom surfaces on 8 July 1995. Nine lures of each type were randomly collected at weekly intervals (0, 7, 14, 21, 28, 35, 42 and 49 d field exposure) for subsequent field testing and chemical analyses.

The average daily emission rate of lures during each time interval was estimated by differential residual analysis (difference between the mean sex pheromone content at the beginning of the time period and the residual values at the end of the time period). Four septa of each type from each date were extracted with 50 ml dichloromethane by shaking lures in a flask for 1 h. The extract was further diluted in dichloromethane and heptane and analyzed with a Hewlett-Packard Model 5880 GC with flame ionization detection (Hewlett Packard, Mountain View, CA) and equipped with a 60 m by 0.32 mm i.d. Supelcowax capillary column (Supelco Inc., Bellefonte, PA) with splitless injection. The oven program used for analysis was: 60 °C for 2 min; ramping at 20 °C/min to 154 °C for 17 min; and a 5-min purge at 210 °C. Recovery rates for E8,E10-12:OH averaged 97 – 102%. The isomeric purity of dispensers was confirmed with a GC- mass spectrometer (Hewlett-Packard model 5970 GC coupled with a HP 5970 mass detector).

The attractiveness of the field-aged septa (0, 7, 14, 21, 28, 35 and 42 d) was evaluated in a commercial apple orchard in July 1996 treated with 1,000 polyethylene dispensers (Isomate-C+, Pacific Biocontrol, Vancouver, WA) per ha. Polyethylene dispensers were loaded with 182.0 mg of a three-component sex pheromone for codling moth (60:34:6 blend of E8, E10-12:OH: dodecanol: tetradecanol). Treatments were arranged in a complete randomized block design. On each date (17, 24 and 31 July and 7 and 14 August) one replicate of each lure type and age was tested. Traps were hung on trees at a height of 3.0 m and spaced 30 m apart.

Unsexed sterile moths were obtained from the codling moth mass-rearing SIR facility in Osoyoos, British Columbia. Moths were sterilized with gamma radiation (33 krad) from a Cobalt$^{60}$ source (dose rate of 1,150-1,320 rad/min) and held at 0 to 2 °C before field release. The sterilized moths had been marked with a red internal dye during larval mass-rearing. Three hundred sterilized codling moths were released around each trap at the beginning of each test by tapping chilled moths out of petri plates onto both the foliage of trees and on the ground within 10 m of each trap. Traps were checked after six nights and only counts of sterilized moths were recorded. Treatments were re-randomized prior to the start of the next replicate.

**Optimizing the attractiveness of gray septa**. Studies were conducted to evaluate the optimal loading rate of gray halo-butyl septa for use in sex pheromone-treated orchards. Gray septa were loaded with varying rates of E8, E10-12:OH (4.0, 10.0, 20.0, and 50.0 mg) by Trécé Inc. (Salinas, CA) personnel using a proprietary technique. Lures were placed in specialized wire hangers and field-aged within an apple orchard situated near Fresno, CA on

12 April 1998. Five lures of each loading rate were collected weekly for 16 wk and kept at –15.0 °C. Field trials to evaluate the attractiveness of these lures were conducted in an apple orchard in Moxee, WA beginning on 19 August and continuing for five wk. One replicate of each lure loading and age was placed in a Pherocon IC trap in a completely randomized 30 x 30 m grid and hung at 3.0 m in the canopy. Each week 300 sterilized moths were released within 20 m of each trap. Traps were checked after six nights and treatments were re-randomized.

**Seasonal comparison of commercial lures.** The two proprietary high-load gray septa, CM Megalure$^{TM}$ and the conventional-load CM L$^{2TM}$, and the standard CM 10X red rubber septa (Trécé Inc., Salinas, CA) were field tested in an apple orchard treated with 1,000 Isomate C+ dispensers per ha from 18 May to 17 August 1999 near Moxee, WA. Lures were placed in Pherocon VI delta traps and eight replicates of each lure type were evaluated in a completely randomized 20 x 20 m grid. Moths were collected and counted, trap liners were replaced, and traps were rotated one position each week. All three septa types were replaced on 6 July. Additionally, the10X septa were replaced on 8 June and 26 July.

**Statistical analyses**. Linear regression analysis was used to fit the emission rate and changes in the % *E,E* isomer as a log decay curve with days aged in the field (Analytical Software 2000). The effects of field aging and dispenser type on moth catch were tested with analysis of variance (ANOVA). Moth count data were transformed (square root [x + 0.05]) to remove heterogeneity of variances before analysis. Means were separated in significant ANOVAs with Fisher's LSD. Differences in emission rate and isomeric purity on specific ages for different dispensers were evaluated with Student t-tests. Linear regression of moth catch on emission rate and % *E,E* isomer were also conducted. The effect of dispenser age and their initial.loading rate for gray septa were evaluated with ANOVA. Specific comparisons were made for 4.0,10.0, and 20.0 mg loads. These data were subsequently grouped and compared with moth catch by 50.0 mg lures. The attractiveness of three proprietary lures was evaluated during the season using ANOVA both on individual dates and for each moth generation.

## RESULTS

**Emission characteristics**. The emission rate from new red rubber septa was nearly five-fold higher than from new gray halo-butyl dispensers (Fig. 1a). The emission rate for each dispenser fit a log decay curve with number of days aged in the field; gray lure: $t = -4.9$, df = 26, $P < 0.001$); and red lure: $t = -8.5$, df = 26, $P < 0.001$. Red septa retained a significantly higher emission rate than gray septa for dispensers aged up to 21 d in the field ($t$ values > 3.45, df = 7, $P < 0.05$). The emission rate for the two dispensers aged from 28-42 d were not significantly different ($P > 0.05$).

The isomeric purity of codlemone loaded in new dispensers was > 96% in both septa types (Fig. 1b). The percentage of the *E,E* isomer remained unchanged in gray septa aged in the field, $t = -1.2$, df = 26, $P = 0.24$. In comparison, the percentage of the *E,E* isomer declined over time in the red septa, $t = -4.6$, df = 26, $P < 0.001$. The combined percentage of the *E,Z* and *Z,E* isomers increased to nearly 20% after 2 wk and 30% after 4 wk.

Field aging (0 – 42 d) of lures was not a significant factor affecting lure attractiveness ($F = 1.47$; df = 6, 56; $P = 0.21$) (Table 1). However, significant differences in the attractiveness of the two lures were found ($F = 9.90$; df = 1, 56; $P = 0.003$). No significant interaction between lure type and age was detected ($P = 0.43$). Gray septa were significantly more attractive than red septa for lures aged for 14 and 42 d (Table 1). Fourteen day-old red lures had nearly three times the emission rate of gray lures (0.22 vs. 0.07 mg/d) ($t = -4.86$, df = 5, $P = 0.003$), and a significantly lower isomeric purity (82.1 vs. 96.2% *E,E* isomer) ($t = 3.47$, df = 5, $P = 0.03$). The emission rates of 42 d-old red and gray lures were low (0.1 mg/d) and

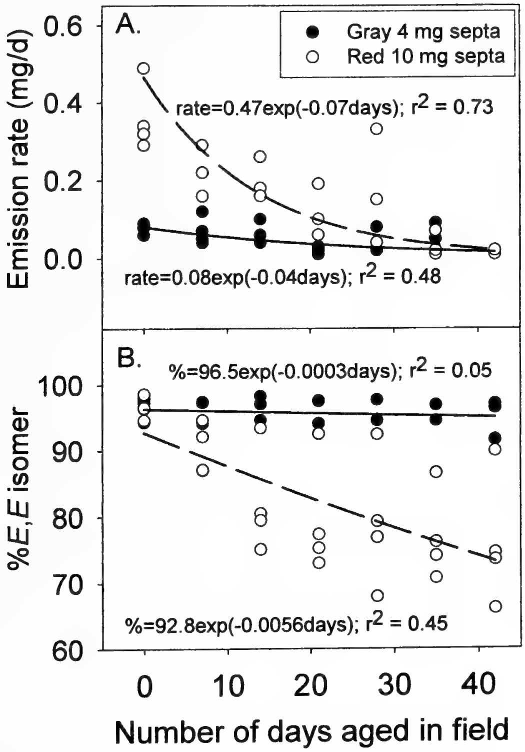

**Figure 1**. Emission rate (**A**) and percentage of the *E,E* isomer (**B**) from field-aged gray halo-butyl elastomer and red rubber septa loaded with 4.0 and 10.0 mg codlemone, respectively. Some data points overlap, n = 4 per date.

**Table 1**

Attractiveness of field-aged gray halo-butyl elastomer and red rubber septa loaded with codlemone tested during July 1996.

| Days aged in the field prior to test | Mean no. (SE) moths per trap | | Statistical analysis | |
|---|---|---|---|---|
| | Red septa | Gray septa | t-value | P-value |
| 0 | 6.4 (2.1) | 5.8 (2.6) | -0.05 | 0.96 |
| 7 | 8.2 (3.6) | 11.6 (3.5) | 0.83 | 0.43 |
| 14 | 1.6 (0.6) | 11.6 (3.8) | 2.93 | 0.02 |
| 21 | 3.0 (1.0) | 7.4 (3.4) | 0.60 | 0.56 |
| 28 | 1.0 (0.3) | 8.2 (2.5) | 2.21 | 0.05 |
| 35 | 2.6 (1.2) | 5.2 (2.2) | 0.42 | 0.68 |
| 42 | 2.2 (0.5) | 7.0 (1.8) | 2.39 | 0.04 |

Red rubber septa and gray halo-butyl elastomer septa were loaded with 10.0 and 4.0 mg codlemone, respectively.

did not differ between lure types ($t$ = -0.28, df = 6, $P$ = 0.79), but the percentage of the *E,E* isomer was again significantly different (76.0 vs. 94.2% for the red and gray lures, respectively, $t$ = 3.48, df = 5, $P$ = 0.03).

The mean number of moths caught per trap with either lure was not linearly correlated to emission rate (gray: $t$ = -0.22, $r^2$ = 0.01, df = 5, $P$ = 0.83; red: $t$ = 1.49, $r^2$ = 0.31, df = 5, $P$ =0.20) (Fig. 2a). A significant difference in moth catch was found between lure types when

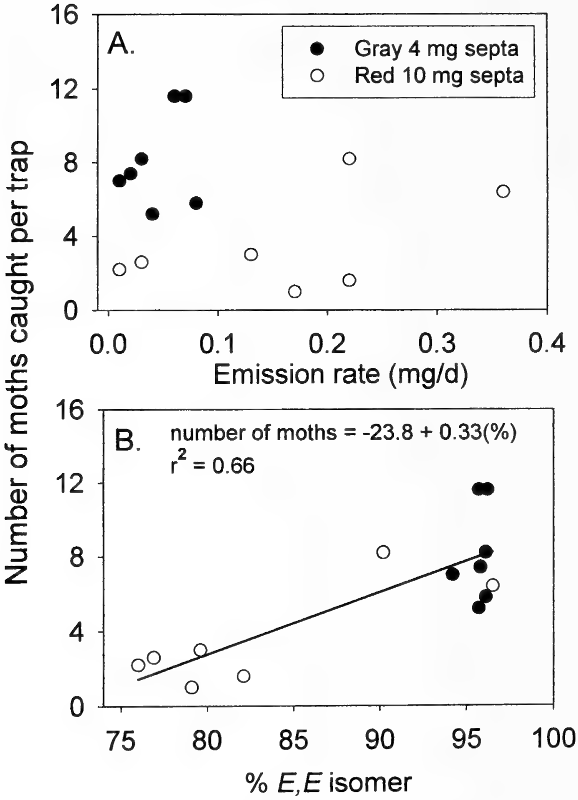

**Figure 2**. Number of moths caught per trap as a function of emission rate (**A**) and percentage *E,E* isomer (**B**) in gray halo-butyl elastomer and red rubber septa loaded with 4.0 and 10.0 mg codlemone, respectively.

the data were pooled across similar emission rates (gray septa 0.01 – 0.08 mg/d and red septa 0.01 – 0.13 mg/d), $t = 4.52$, df = 8, $P = 0.004$. Within this lure emission range, moth catch in traps baited with gray versus red septa was more than three-fold higher (Fig. 2a).

A significant linear relationship was found between mean moth catch and the percent *E,E* isomer for red septa, $t = 3.23$, df = 5, $r^2 = 0.68$, $P = 0.02$. No similar relationship was found for moth catch and percent *E,E* isomer for gray septa, $t = -1.18$, df = 5, $r^2 = 0.22$, $P = 0.29$. Combining the data for both lures generated a significant relationship between moth catch (y) and the percent *E,E* isomer (x): $y = -23.8 + 0.33x$, $t = 3.76$, df = 12, $r^2 = 0.66$, $P = 0.0003$. These data fall into two distinct groups based on the percentage of *E,E* isomer (Fig 2b). Lures containing > 90% *E,E* isomer caught on average four-fold more moths than lures emitting < 85% *E,E* isomer, $t = 5.69$, df = 12, $P = 0.001$.

**Optimizing the Loading Rate of Gray Halo-butyl Septa.** Dispenser age ($F = 5.03$; df = 7, 128; $P < 0.0001$) and pheromone loading ($F = 8.69$; df = 3, 128; $P < 0.0001$) of gray septa were both significant factors affecting moth catch (Table 2). The interaction between lure age and pheromone load was not significant ($P = 0.87$). A significant curvilinear decline in moth catch with lure age was detected with the nontransformed data, $F = 4.72$,; df = 1, 128 ; $P = 0.03$. Moth catch among the 4.0, 10.0 and 20.0 mg loads was not significantly different ($F = 0.17$; df = 2, 128; $P = 0.85$). Moth catch with the 50.0 mg lure was significantly different from the other three lure loads ($F = 25.75$; df = 1, 128, $P < 0.0001$) and declined linearly with age ($t = -2.71$, df = 37; $P = 0.01$). Moth catch by 50 mg lures aged for 2 wk was significantly greater than with older lures and a curvilinear relationship was suggested ($t = 1.96$, df = 37;

$P = 0.57$). Mean moth catch by gray lures loaded with 4.0 – 20.0 mg codlemone aged up to 10 wk did not differ significantly from moth catch by new 10X red rubber septa (Table 2; see means lacking asterisks). In comparison, moth catch by aged 50.0 mg gray septa did not differ from 10X red septa over the 16 wk.

**Seasonal comparison of lures.** The attractiveness of the two proprietary grey septa lures, CM Megalure$^{TM}$ and CM L$^{2\,TM}$, and the CM 10X red rubber septa did not differ until the third wk of the study (Table 3). During the third wk, moth catch was significantly higher in traps baited with the Megalure$^{TM}$, and the L$^{2\,TM}$ lure caught more moths than the 10X lure. The 10X lure was replaced on 8 June and no difference in the attractiveness of lures was found the following week (17 June) (Table 3). Mean moth catches in traps baited with the 10X lure were >75% lower than in traps baited with the Megalure$^{TM}$ for wk two and three (23 and 29 June) though not significantly different ($P$ values = 0.07-0.08). After three wk the 10X lure caught significantly fewer moths than the Megalure$^{TM}$. All lures were replaced on 6 July and moth catch was again significantly lower in traps baited with the 10X vs. the Megalure$^{TM}$ after two wk (19 July). The 10X lure was replaced on 26 July and caught significantly fewer moths than the Megalure$^{TM}$ after two wk (10 August). The L$^{2\,TM}$ lure caught an intermediate number of moths in comparison with the other two lures throughout the season (Table 3).

**Table 2**

Comparison of mean (SE) captures of codling moth in sticky traps baited with halo-butyl gray septa loaded with varying amounts of codlemone in a sex pheromone-treated apple orchard in Moxee, WA.

| | Pheromone Load (mg) | | | |
|---|---|---|---|---|
| Lure age (wk) | 4.0 | 10.0 | 20.0 | 50.0 |
| 2 | 21.2 (12.7) | 12.2 (4.7) | 12.2 (8.0) | 32.4 (7.1) |
| 4 | 7.6 (2.1) | 10.6 (6.0) | 8.8 (3.7) | 15.8 (6.3) |
| 6 | 6.0 (1.6) | 9.6 (3.3) | 5.6 (2.5) | 14.8 (2.2) |
| 8 | 5.6 (3.7) | 4.0 (1.9) | 7.4 (3.2) | 13.2 (4.0) |
| 10 | 5.0 (1.4) | 8.2 (2.0) | 6.4 (4.2) | 11.6 (5.5) |
| 12 | 1.0* (0.3) | 2.8* (1.2) | 3.6* (2.4) | 9.2 (4.2) |
| 14 | 1.6* (0.8) | 5.8 (2.0) | 3.6* (1.0) | 7.6 (3.2) |
| 16 | 1.8* (0.8) | 2.0* (0.7) | 0.6* (0.4) | 9.2 (4.8) |

Mean catches followed by '*' were significantly different ($t$-test, df = 8, $P < 0.05$) from the mean (SE) catch with new, red rubber septa loaded with 10.0 mg E8,E10-12:OH, 20.2 (6.6) moths per trap.

## DISCUSSION

The chemical instability of conjugated dienes, such as codlemone in sulphur-cured red rubber septa is well known (Brown and McDonough 1986, Ideses and Shani 1988, Vrkoč *et al.* 1988). Yet, despite this general knowledge, a red rubber septum has been the standard lure used to monitor codling moth for nearly 30 yr (Riedl *et al.* 1986). More recently, the use of a 10.0 mg red septa for monitoring codling moth in orchards treated with sex pheromone dispensers has been widely reported in North America (Knight 1995a, Judd *et al.* 1996, Gut and Brunner 1998) and Europe (Charmillot 1990). Gut and Brunner (1995) found that these high-load lures require frequent replacement and presumed this was caused by a rapid drop in their emission rates under sustained warm summer weather. Our data suggest that the 10X septa are attractive for 1- 2 wk; however, their rapid loss in attractiveness appears to be due to the degradation of codlemone and not to a reduction in their emission rate. Similar results emphasizing the importance of the chemical instability of conjugated dienes in rubber

**Table 3**

Seasonal comparison of three commercial lures (n = 8) rotated weekly within a 12 ha apple orchard treated with 1,000 Isomate C+ dispensers per ha.

| Date traps checked | Mean catch (SE)<br>Red septa<br>10X | <br>Gray septa<br>MegaLure$^{\text{TM}}$ | <br>Gray septa<br>$L^{2\,\text{TM}}$ | Statistical analysis<br>$F_{2,21}$ | <br><br>$P$ value |
|---|---|---|---|---|---|
| 25 May | 1.63 (0.68) | 2.88 (0.95) | 1.88 (0.58) | 0.59 | 0.56 |
| 01 June | 0.13 (0.13) | 0.63 (0.18) | 0.50 (0.27) | 1.85 | 0.18 |
| 08 June | 0.00* (0.00)a | 2.25 (0.67)c | 0.88 (0.23)b | 11.00 | <0.001 |
| 17 June | 1.00 (0.33) | 1.88 (0.40) | 0.88 (0.64) | 2.08 | 0.15 |
| 23 June | 0.50 (0.27) | 2.13 (0.67) | 0.75 (0.49) | 2.94 | 0.08 |
| 29 June | 0.13 (0.13) | 1.00 (0.38) | 0.50 (0.19) | 2.98 | 0.07 |
| 06 July | 0.13* (0.13)a | 1.25* (0.41)b | 0.25* (0.16)a | 4.95 | 0.02 |
| **Total 1st flight** | **3.52 (0.82)a** | **12.02 (1.30)b** | **5.64 (1.03)a** | **12.81** | **<0.001** |
| 12 July | 1.75 (0.75) | 1.63 (0.57) | 3.00 (0.89) | 0.98 | 0.39 |
| 19 July | 0.00 (0.00)a | 1.63 (073)b | 0.38 (0.18)ab | 4.69 | 0.02 |
| 26 July | 0.13* (0.13)a | 4.25 (1.26)b | 4.38 (1.84)b | 6.02 | 0.01 |
| 03 August | 3.25 (0.98) | 4.50 (1.69) | 5.00 (0.89) | 0.60 | 0.56 |
| 10 August | 3.13 (1.48)a | 16.13 (3.89)b | 6.75 (1.51)a | 8.74 | 0.002 |
| 17 August | 2.38 (1.69)a | 10.75 (2.74)b | 7.00 (3.70)ab | 3.45 | 0.05 |
| **Total 2nd flight** | **10.64 (2.52)a** | **38.89 (6.17)c** | **26.51 (4.85)b** | **4.18** | **0.03** |

Traps were placed in the orchard on 5 May in a completely randomized 20 x 20 m grid. Traps were moved one position within the grid each week. Lures of each type were replaced on dates designated with a '*'. Data were transformed (sqrt(x+0.5) and subjected to ANOVA. Weekly means followed by a different letter were significantly different, $P < 0.05$, Fishers LSD.

substrates were found with red rubber septa loaded with (*E,E*)-8,10-dodecadien-1-yl acetate, the sex pheromone for the pea moth, *Cydia nigricana* (F.) (Horák *et al.* 1989).

The inhibitory effects of the isomeric blend of 8,10-dodecadien-1-ol on the attraction of codling moth was first shown by Roelofs *et al.* (1972) and later by McDonough *et al.* (1993). El-Sayd *et al.* (1998) demonstrated that this inhibitory effect was due to the presence of the *E,Z* isomer. McDonough *et al.* (1993) suggested that this reduction in attractiveness would be amplified in the high load lures used to monitor sex pheromone-treated orchards unless codlemone was stabilized. Isomerization of codlemone can be minimized by adding antioxidant or antiultraviolet components (Millar 1995) or by avoiding substrates containing sulphur (Brown and McDonough 1986). Horák *et al.* (1989) increase the longevity of lures for pea moth by using rubber substrates cured with organic peroxides instead of sulphur. Brown and McDonough (1986) found that isomerization of codlemone in gray halo-butyl elastomer septa was 4.7-fold slower than in red rubber septa. The gray halo-butyl septa appears to be a more effective lure than the red rubber septa for monitoring codling moth in sex pheromone-treated orchards due to this reduced rate of isomerization of codlemone.

The optimal loading rate of gray septa to monitor codling moth is difficult to determine from these studies. Moth catch as a function of lure age was curvilinear across the range of sex pheromone loads tested, with the highest moth counts for each pheromone load being found in traps baited with two-wk-old lures. Gray septa loaded with 4.0 – 50.0 mg codlemone all effectively monitored codling moth for at least 10 wk. The 50 mg lure caught significantly more moths than the other three lures, and its attractiveness most closely matched the mean moth catch by new 10X red septa over a 10 wk period. Residual studies of septa aged at 24 °C in the laboratory demonstrated that the half-life of codlemone in gray septa is 2.6-fold longer than in red septa (unpublished data). The emission rate of alcohol sex pheromones from rubber septa has been shown to be proportional to the amount of pheromone present, i.e., first-order process (Butler and McDonough 1981). Therefore, one can estimate that the emission rates from gray septa loaded with 26 mg and a red septa loaded 10 mg codlemone should be roughly equivalent.

Replacing the standard red rubber septa with the gray halo-butyl lure appears to be a promising alternative for monitoring codling moth in sex pheromone-treated orchards. However, this switch may require some changes in the established action thresholds for supplemental insecticide sprays during both generations. Current recommendations provide a narrow range (2.5-fold) of cumulative moth catch to trigger the need for supplemental sprays (Gut and Brunner 1996). In comparison, cumulative catches of codling moth by the Megalure$^{TM}$ were more than three-fold higher than with the 10X red lure during both moth flights despite frequent lure replacements of the red septa (Table 3). Development of a codling moth lure that can minimize the occurrence of 'false negatives' (absence of moth catch despite the occurrence of fruit injury) is likely more important than having to change the catch threshold for applying supplemental controls. Previous studies have examined the effects of trap placement (Knight 1995b) and the proximity of the monitoring trap to the sex pheromone dispenser on lure performance (Knight *et al.* 1999). Optimizing the use of the gray septa to provide long-lasting effective monitoring in sex pheromone-treated orchards may require further refinements. Alternatively, development and testing of new lure substrates and attractants could further minimize the risks associated with the use of sex pheromones to manage codling moth.

## ACKNOWLEDGEMENTS

I would like to thank Bill Lingren and D. Rajapaske Raja (Trécé Inc., Salinas, CA) for providing the proprietary lures, Ken Bloem (Sterile Insect Rearing Facility, Osoyoos, British Columbia) for providing the sterilized codling moths, John Turner and Kathi Johnson (USDA, ARS, Wapato, WA) for assisting in the field work, and Dave Horton (USDA, ARS, Wapato, WA) for help with the statistical analyses. This project was partially funded by the Washington Tree Fruit Research Commission (Wenatchee, WA).

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# A new species of *Boreus* (Mecoptera: Boreidae) from Vancouver Island, British Columbia

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## ABSTRACT

*Boreus insulanus* Blades (Mecoptera: Boreidae), a new species from Vancouver Island, British Columbia, Canada, is described and distinguished from similar species using morphological characters and measurements. Similarities of male genitalic structures, the notched ninth sternum and male wings abruptly narrowed at the middle place this new species in the *brumalis* subgroup of the *nivoriundus* group of *Boreus* species. The *brumalis* subgroup currently includes *B. brumalis* Fitch, *B. nix* Carpenter, *B. pilosus* Carpenter, and *B. bomari* Byers. Characters that distinguish *Boreus insulanus* from these related species include: fine appressed hairs above the eyes, on the pronotum, and wings; absence of fine, erect hairs on pronotum, wing and abdominal sclerites; relative position and number of pronotal bristles (4 anterior; 4 posterior); and dark abdominal sclerites with a metallic green sheen. The distributional records for this new species indicate that it may be confined to Vancouver Island's interior mountain range.

## INTRODUCTION

Species of *Boreus,* commonly called snow scorpionflies, inhabit mountainous regions of Europe, northern Asia, and North America. They are usually associated with mosses and are unusual in that the adults mate and disperse during the winter months (November to March) (Penny, 1977; Hagvar, 2001). Specimens are often collected on snow during sunny, warm days, but recent research on *B. hyemalis* (L.) shows that activity on the snow surface is greatest on windless, cloudy days and that most activity during the winter occurs in air pockets under the snow pack (Hagvar, 2001). Penny's (1977) comprehensive systematic study of the family provides detailed descriptions and taxonomy of the known species and the biology of the group. More specific studies on the biology of North American species include works by Cooper (1974), Shorthouse (1979), and Courtin *et al.* (1984). *Boreus* species described since 1977 include *B. jacutensis* Plutenko and *B. tardokijanensis* Plutenko from Russia (Plutenko, 1984; 1985) , *B. jezoensis* Hori and Morimoto from Japan (Hori and Morimoto, 1996) and *B. bomari* Byers and Shaw from Wyoming, USA (Byers and Shaw, 1999).

This paper describes a new species of *Boreus* found in collections carried out by the author on private property at Camas Hill, Metchosin, on the southern tip of Vancouver Island, British Columbia (48° 23' 57" N 123° 35' 44" W). Specimens were collected using continuous pitfall trapping over a period of two years. Specimens of this new *Boreus* appeared in samples from January to March 2000, and November 2000 to March 2001. Literature research into the genus and inquiries to various collections in North America failed to uncover any records of *Boreus* from Vancouver Island (Penny, 1977; Blades, unpublished data). Searching of the Royal BC Museum collection uncovered two more specimens from Vancouver Island. Using Penny's (1977) key and descriptions, original descriptions (Carpenter, 1935), and literature on recently described species (Hori and Morimoto, 1996; Byers, 1999), I determined that these specimens represented a new species. This paper describes this new species of *Boreus* and provides diagnostic characters to distinguish it from other nearctic *Boreus*.

Specimens were examined in detail and compared using measurements and characteristics of external morphology. Measurements of overall body length were made but the obvious distension of the specimens limits the usefulness of this character in comparisons with other species, a problem also noted by Penny (1977). Instead, only lengths and ratios of rigid structures such as the head, eye, wing, ovipositor and dististyle were considered when making comparisons with other species. Characteristics of the male genitalia in the new species were similar to those of *B. pilosus* Carpenter and *B. nix* Carpenter. This similarity and the notched ninth sternum and male wings abruptly narrowed at the middle place this new species in the *brumalis* subgroup of the *nivoriundus* group of species as defined by Penny (1977). The *brumalis* subgroup includes *B. brumalis* Fitch, *B. nix*, *B. pilosus*, and *B. bomari* Byers (Penny 1977; Byers 1999). Twelve hundred and seventy eight specimens of ten related species (including paratypes) were obtained from various North American collections for additional comparisons.

## SPECIES DESCRIPTION

*Boreus insulanus* n. sp.
(Figs. 1 to 7)

## TYPE MATERIAL

**Holotype male:** Canada. British Columbia: Vancouver Island, Metchosin, summit of Camas Hill (293 m; 48° 23' 57" N 123° 35' 44" W), sample CH99-18P, yellow pantrap, 13II to 13 III 2000, D. Blades, C. Reznechenko and L. Rosenblood. Deposited at the Royal British Columbia Museum (RBCM); specimen number ENT000-000314.

**Paratypes:** Same location as holotype. 2 males, 1 female, 3 I to 13 II 2000; 3 males, 13 II to 13 III 2000; 1 male, 5 to 13 XI 2000 deposited at RBCM; 3 males 13 II to 13 III 2000 deposited one at each of: The Snow Museum (RBCM #ENT000-000310), University of Kansas; the Canadian National Collection (CNC), Ottawa (RBCM #ENT000-000312); and the California Academy of Sciences, San Francisco (RBCM #ENT000-000309). Remaining specimens (6 males, 1 female; 9 XII 2000 to 8 III 2001) retained in author's collection, to be deposited at CNC by December 2004.

## ADDITIONAL MATERIAL

Two female specimens with characteristics clearly matching those of type specimens: one from Goldstream, near Victoria (48° 23' N 123° 33' W; pinned) collected by G.A. Hardy, 7 III 1927 (RBCM #ENT991-164463); and one from north side of Mount Cokely at 1500 m, near Port Alberni ( 49° 14' 23" N 124° 35' 12" W ; in alcohol) collected by S.G. Cannings, 23 IV 1995 (RBCM #ENT998-010684).

## ADULTS

General: A large species of *Boreus,* length of males 3.9 to 6.6 mm (avg 4.7 mm) (Fig. 1) and females 5.4 to 6.0 mm (avg 5.8 mm) preserved in alcohol, 5.0 mm for pinned female (measured in lateral view from tip of ovipositor/sternum 9 of male to base of antenna). Abdominal sclerites, wings and occiput dark brown to almost black with a green metallic sheen. Thorax, legs and rostrum lighter, varying from tan to dark brown; the legs lighter in colour than thorax. Colours of pinned specimen similar to those in alcohol. Immature stages unknown. Terms used in this description follow those of Penny (1977) and Byers (1999); it is important to note that setae and bristles (=strong setae) possess ring-shaped

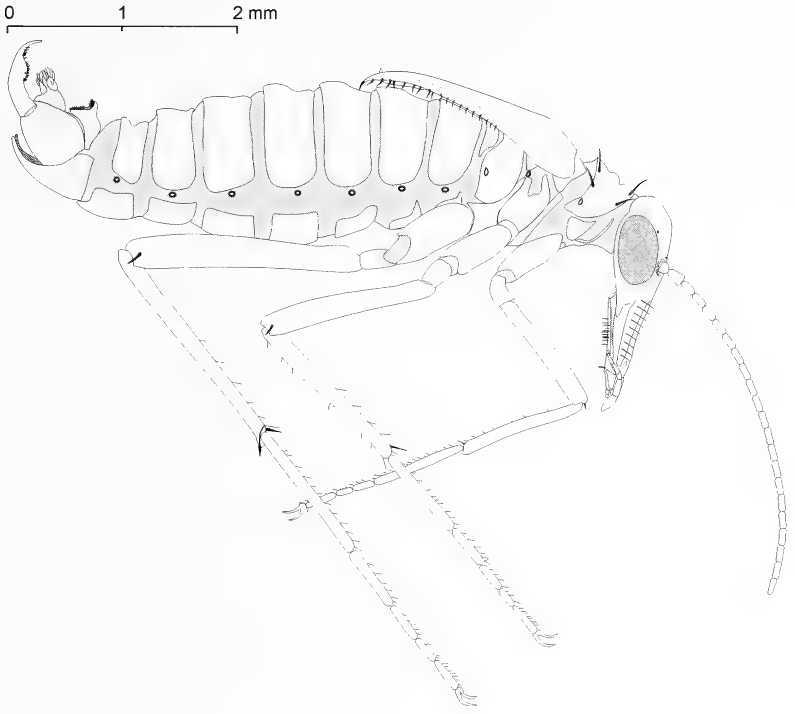
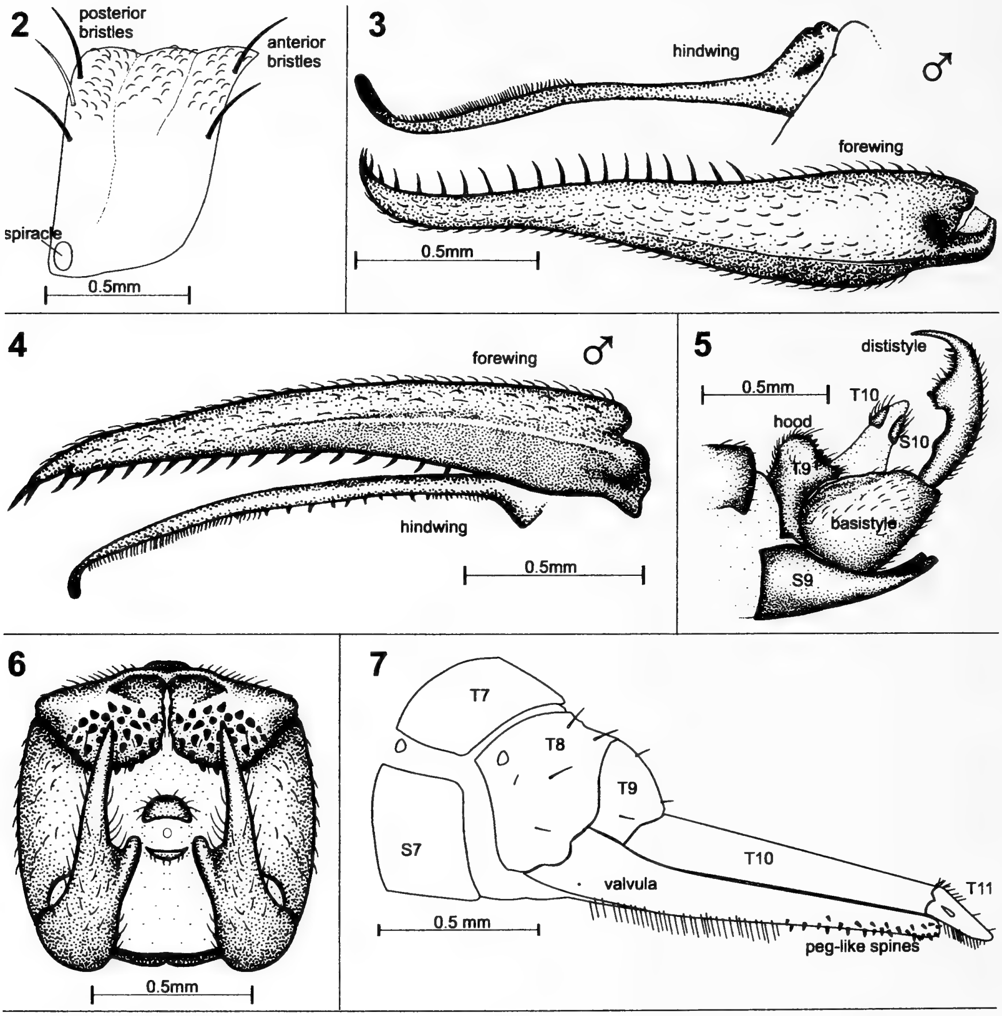


**Figure 1**. Lateral view of male *Boreus insulanus* indicating setae and bristles; hairs, and setae of palps, omitted.

basal sockets whereas hairs and spines do not.

Head: Head coloration dark from top of head to just below eyes on sides and down front of face almost to tip of rostrum. Lateral and posterior areas of rostrum tan to light brown; an abrupt, horizontal separation of light and dark colours just below eye when viewed in profile. Eyes reddish. Length of head from vertex to tip of rostrum: 1.57 to 2.00 mm (avg 1.81 mm) in males; 1.88 to 2.07 mm (avg 1.96 mm) in females. Diameter of eye measured in same direction as head: 0.50 to 0.68 mm (avg 0.62 mm) in males; 0.58 to 0.67 mm (avg 0.63 mm) in females. Ratio of maxillolabial complex to rostrum varies from 0.89 to 0.97 (avg 0.93) in male and from 0.85 to 0.93 (avg 0.88) in female. Occipital region glabrous, finely wrinkled and without hairs or setae. Area between eyes and occiput with short, fine, recurved hairs closely appressed to the head. Fine, erect, white hairs dominate the area between the eyes and below the antennal sockets. A few fine, pale, erect setae present on base of rostrum (frons) below antennal sockets (about 0.06 mm in length). A distinct row of 10-12 such setae in furrows (depressions) on either side of the otherwise bare midline of rostrum. Mentum with 12 to 20 or more setae similar in length, but slightly thicker, to those in lateral furrows; situated primarily in basal half, with two near distal margin. Lateral ocelli nearly touching compound eyes with smaller median ocellus present near bases of antennae. Antennae brown; with 20 to 22 (mode=20) flagellar segments in males; 19 to 21 (mode=19) in females.



**Figures 2 to 7**. 2) Lateral view of pronotum of *Boreus insulanus* showing position of bristles and appressed hairs. Gray bristle indicates position of occasional intermediate bristle. 3) Dorsal view of male *Boreus insulanus* hindwing and forewing. 4) Lateral view of male *Boreus insulanus* forewing and hindwing. 5) Lateral view of male *Boreus insulanus* genitalia. T=tergum; S=sternum. 6) Dorsal view of male *Boreus insulanus* genitalia. 7) Lateral view of *Boreus insulanus* ovipositor and adjacent segments, indicating position of setae, hairs and peg-like spines. Illustrations 3, 4, 5 and 6 by D. Young.

Thorax: Anterior margin of pronotum with two dorsolateral bristles and usually two lateral bristles; posterior margin with two dorsolateral, two lateral, and rarely, two sublateral bristles (Fig. 2). Pronotum with two obscure transverse furrows and covered by short recurved hairs, closely appressed to the surface. Mesonotum, metanotum and lateral thoracic sclerites without conspicuous bristles or hairs in male. Females with a pair of short, cruciate bristles near center of mesonotum.

Legs: Colour of coxa same as adjacent lateral sclerites; remaining leg segments lighter brown to yellowish. Stout, dark brown, apicofemoral spine present. Anterior faces of coxae and trochanters with abundant long white hairs. Remaining leg segments covered in short, fine hairs and armed on ventral surface with two rows of evenly spaced, short, fine, erect setae. Each tibia with two apical spurs. All tarsi with two simple, terminal claws. Ratio of lengths of foreleg to midleg to hindleg approximately 1 : 1.3 : 1.7. Hindleg approximately 1.5 times body length in males; in female about equal to length of body including ovipositor.

Wings: Male forewings darker brown than thorax; outer margins distinctly narrowed near middle in dorsal view (Figs. 3 and 4). Length of wing 1.60 to 2.13 mm (avg 1.83 mm). Each forewing bears 17 to 24 (mode=18) strong, black, slightly twisted, outer spines starting about one-third of length from base and increasing in size from 0.05 mm to 0.11 mm at the wing tip. Inner forewing spines similar in shape, size and position to outer spines, and numbering between 17 and 26 (mode=19) on each wing. Terminal forewing spine strongly incurved and about the same length as pronotal bristles (0.16 mm). Forewing rugulose and covered by fine hairs, recurved and closely appressed to the dorsal surface. Hindwing light brown and tubular in basal four-fifths and becoming black and flattened at point of sharp incurving to tip. Middle portion of hindwing bears 7 to 12 (mode=10) short, stout spines with longer fine hairs intermixed. Distal half of hindwing before curved tip with felt-like pad of short, yellow to orange hairs. Female forewings short (avg 0.4 mm), oval, brown and covered with fine hairs, recurved and closely appressed to the surface. Hindwings very small and completely overlapped by the forewings.

Abdomen: Terga and sterna dark brown to almost black with metallic green sheen and densely covered in short, fine, semi-erect, posteriorly directed hairs that are clearly visible when backlit. Intersegmental membranous areas white. All segments with unfused terga and sterna. Female abdomen clearly larger in diameter than male but otherwise similar for segments 1 to 7.

Male genitalia (segments 8 to 10): Segment 8 unmodified, similar in appearance to segment 7 (Fig. 5). Tergum 9, sternum 9, basistyles and dististyles very dark brown to black. Sternum 9 long, extending to junction of basistyle and dististyle, and bearing a shallow, but distinct, notch along the posterior margin. Tergum 9 in profile with low hood that acts as a receptacle for the tips of the dististyles. In dorsal view the hood appears as a U-shaped ridge, forming a cup-like invagination, surrounded posterolaterally by the denticles (Fig. 6). The hood bears long, fine, pale hairs on the inside vertical surfaces (also visible in lateral view) and a pair of median bare areas, separated by a septum, where the dististyles touch. Denticles and surrounding cuticle black and difficult to see, especially when dististyles retracted into hood. Number of denticles ranged from 17 to 32 (mode=20) on each of the denticular areas of tergum 9. Dististyle with sharp tip, a medial, thumblike projection and a medial row of 14 to 21 (mode=21) short spines along inner margin. Tergum and sternum 10 small, oval, brown sclerites each bearing a few fine hairs. Membranous gonopore situated ventrally to the more prominant anus and usually hidden in the retracted state.

Female genitalia (segments 8 to 11): Configuration of terminal segments similar to females of other *Boreus* species (Fig. 7). Tergum 8 with fine transverse wrinkling and nearly encompassing segment 8, the sclerite ending just before venter where the valvulae emerge. Tergum 9 smooth and shorter than preceeding and following segments. Segment 10 about 1 mm in length, equal to the length of the maxillolabial complex, and lacking hairs or setae on dorsal surface. A few scattered setae present on dorsal surfaces of segments 8, 9 and 11. Segment 11 and cerci fused into short, triangular segment. Ventral ovipositor valves (valvulae of segment 8) with numerous long, fine, white hairs on basal

2/3 to 3/4; replaced by about 30 to 40 evenly spaced, short, peg-like spines in terminal region. These spines lack emergent terminal hairs evident in other species (Penny, 1977; Byers, 1999) but longer hairs are occasionally present between the peg-like spines.

## DIAGNOSIS

Presence of pronotal spines, notched sternum 9 of male, male wings narrowed near middle and configuration of male genitalia place this species in the *brumalis* subgroup with *B. nix*, *pilosus*, *brumalis,* and *bomari*. It is distinguished from these other species by the following combination of characteristics: head and abdomen dark brown to black with a distinct metallic green sheen, wings darker than brown thorax, legs light brown to yellowish and clearly lighter than thorax; fine hairs above eyes, on pronotum, and wings, recurved and appressed to surface; pronotal margins with two or four anterior and four posterior bristles, these bristles strong, dark and slightly curved; pronotum lacking erect, pale, intermediate length setae or hairs; distinct, erect hairs also absent from wings, occipital area, and sclerites of thorax and abdominal segments 1 – 8; 17 to 24 outer forewing spines; 17 to 26 inner forewing spines; 17 to 32 denticles; 14 to 21 dististyle spines; antenna with 19 to 22 flagellar segments; ovipositor equal in length to maxillolabial complex; tergum 10 of female without dorsal hairs or setae; terminal peg-like spines of valvulae without emergent hairs.

## ETYMOLOGY

The latin word for "islander", *insulanus,* was chosen to indicate the apparent restriction of the species' range to Vancouver Island.

## DISTRIBUTION AND HABITAT

This species is apparently confined to Vancouver Island and is currently the only *Boreus* species known from the island (Penny 1977 ; Blades unpublished data). Collection locales are situated along the interior mountain range of Vancouver Island at elevations from 300 to 1500 m. Like other *Boreus* species, it is believed to be associated with mosses.

## ACKNOWLEDGEMENTS

I would like to thank Catherine Reznechenko and Lorne Rosenblood for hosting my study of insect diversity on their property at Camas Hill, Metchosin. I would also like to thank David Young for his contributions to the illustrations in this paper and Robert Cannings for his helpful comments on the manuscript and his moral support. Thanks are also extended to the many people who responded to my requests for distributional records and specimens from their collections – full acknowledgements to these people and their institutions will appear in an upcoming paper on *Boreus* distributions in western North America. I would also like to thank Richard Zack for supplying specimens of another undescribed species of *Boreus* during preparation of this description.

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# Erratum

# Insect population ecology in British Columbia

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In Volume 98, pp. 107-108, the historical account relating to the work of Neil Gilbert and collaborators was not correct. Neil wrote the following response:

‘After cabbage aphid and *Masonaphis*, I thought it might be possible to introduce some limited generalization into population dynamics by constructing a Universal Aphid of which every aphid species would be a particular case. But pea aphid put paid to that. In the first two species, predation could be represented by a simple formula because it only took surplus production of aphids and was more or less compensated by density-dependent reproduction. In pea aphid, the coccinellids drove aphid numbers down low, so we either had to study predation in detail or admit defeat. It was all very messy but proved possible to predict predation rates, but not the numbers of beetles entering the field. That would be possible only if you knew the dynamics of the whole local ecosystem, an impossible task. In other words, the aphid population could not be isolated from the rest, even to a first approximation. The whole thing was a failure as far as I was concerned, although a very instructive one.’

# Erratum

# Behavioural and chemical ecology in British Columbia

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Volume 98, p 113, paragraph 5, lines 1-5 should read:

The second major development was the formation of the Pestology Centre at Simon Fraser University (SFU) in 1967. Several members of the centre focused on behavior including, Bert Turnbull (predators), John Borden (host and mate-seeking behaviors), Peter Belton (acoustic and oviposition behaviors in mosquitoes), Manfred Mackauer (behavior of parasitoids) and Bryan Beirne (behavior of biocontrol agents).

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# Journal of the Entomological Society of British Columbia

Volume 99 Issued December 2002 ISSN #0071-0733